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Evaluation of the taproot elongation rates of soybean cultivars

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EVALUATION OF THE TAPROOT ELONGATION RATES OF SOYBEAN CULTIVARS

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Evaluation of the taproot elongation rates of soybean cultivars

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INTRODUCTION

Water deficit stress is one of the major factors limiting crop production in the world. In many regions, drought is a normal part of the climatological pattern. Furthermore, even in areas with abundant rainfall, soil moisture supplies are rarely at optimum levels during the growing season. In fact, even if the soil water content is near field capacity, evaporative demand may still exceed water uptake by the plant. Whenever this happens, plant water potentials decrease and plant processes are adversely affected. Thus, wherever crops are grown, water deficit stress can limit growth and yield.

Because of the widespread occurrence of water deficit stress, numerous mechanisms have evolved in plants that modify or limit the effects of water stress. In general, these mechanisms usually involve increasing water uptake, decreasing transpiration, hastening maturity, or tolerating low plant water potentials. The water stress resistance of a particular plant species, however, usually involves many mechanisms and the importance of each mechanism to the success of the plant is often difficult to assess. Obviously, from a crop breeding perspective, knowing which plant characteristics are important for water stress resistance could be extemely valuable. Therefore, scientists have devoted much research to the physiological processes and the genetic variability of water stress resistance mechanisms, in the hope of finding plant characteristics that can improve water stress resistance of crop species.

In order to evaluate the importance of a quantitative plant characteristic to the water stress resistance of a crop species, individuals that express the characteristic to varying degrees or levels must be found and their water stress resistance measured under drought conditions in the field. One way to obtain plants that express a range in a characteristic is to cross two individuals that differ drastically for that trait and then examine the progeny. The progeny of this cross should express the trait at many levels. The importance of the trait to water stress resistance of the plant species could then be determined by comparing the level of expression of the trait with the degree of water stress resistance of the progeny in the field. In order to accomplish this, a standardized procedure must be developed to accurately measure the degree of expression of the trait to be examined. Measurement of the trait is necessary, both to find suitable parental lines and to evaluate the progeny. Additionally, the measurement must be reproducible and must correlate with real differences among genotypes in the field.

A research group at Iowa State University has been examining the root systems and water uptake patterns of soybeans with the goal of improving soybean drought avoidance. Data are being gathered to determine (a) which root system characteristics control water uptake, (b) whether the genetic variability of these characteristics is great enough to allow selection, and (c) how environmental factors affect the expression of root system characteristcs.

The purpose of this study was (a) to develop a standardized

procedure for evaluating soybean taproot elongation, (b) to evaluate in the field the rooting and water uptake patterns of soybean cultivars with widely differing taproot elongation rates in the glasshouse, and (c) to examine the effect of seed, plant, and cultural factors on taproot elongation rate.

Explanation of Dissertation Format

This dissertation follows the "alternate" format and consists of four parts. The first part is a literature review of plant adaptations to drought and attempts to screen crop plants for drought resistance. The second and third parts are manuscripts that will be submitted for publication to Agronomy Journal. The fourth part is a general summary of the entire dissertation. Both manuscripts are co-authored by Dr. Richard M. Shibles and Dr. Howard M. Taylor, who advised in the conduct of the studies and the preparation of the manuscripts.

LITERATURE REVIEW

Adaptations of Crop Plants to Drought

Introduction

Drought can be defined as the absence of rainfall for a period of time long enough to deplete soil moisture to levels at which damage to plants occurs (Kramer, 1980). In terms of crop production, drought is a lack of rainfall that causes a reduction in potential yield (Kramer, 1980; Blum, 1980). Similarly, water deficit stress can be defined as the combination of environmental factors capable of producing potentially injurious strain on plants due to water loss (Levitt, 1980). Or in other words, water deficit stress is the set of conditions, usually including drought, that cause plants to lose water faster than they can obtain it. Therefore, drought stress is water deficit stress, caused by lack of rain.

In any case, water stress or drought stress, whether over a period of a few hours or several months, can seriously impair many plant functions associated with their survival, growth, and reproduction success (Hsiao, 1973; Hsiao et al., 1976a; Levitt, 1980). Unfortunately, the manner in which these damaging effects of drought stress combine to cause a reduction of yield in agricultural systems is not clearly understood (Hsiao et al., 1976b). Furthermore, various genotypes within a crop species will often yield better than others depending on the severity and phenological timing of the drought (Blum, 1973; Fischer and Maurer, 1978). In most cases, however, the

characteristics that provide a particular genotype with a yield advantage under a given set of conditions are not immediately obvious. As a result, researchers can only attribute the drought advantage of these genotypes to their physiological, developmental, or morphological characteristics that are similar to the known drought adaptations of plants native to arid environments.

Plant adaptations to drought are thought to be the result of phylogenetic evolution of different ecotypes within a species (Steponkus et al., 1980). Many attempts have been made to classify plant adaptions to drought (Maximov, 1929; May and Milthorpe, 1962; Parker, 1968; Arnon, 1975; Levitt, 1980), but few if any genotypes can be assigned to any one category. To avoid confusion, a modified version of the classification system developed by Levitt (1980; Fig. 1) will be used as a basis for discussion. The three principal categories of drought adaptation in this system are: (1) drought escape, (2) water stress avoidance, and (3) water stress tolerance.

Drought escape

In desert plant communities, there is a wide range of species, called ephemerals, that complete their entire life cycles within a short period of adequate water supply. Two characteristics of desert ephemerals that are important to their survival are rapid phenological development and developmental plasticity (Turner, 1979).

Rapid phenological development The drought escaping ability of some crop species depends on rapid phenological development. For example, earliness allows small grain crops, especially wheat (Triticum

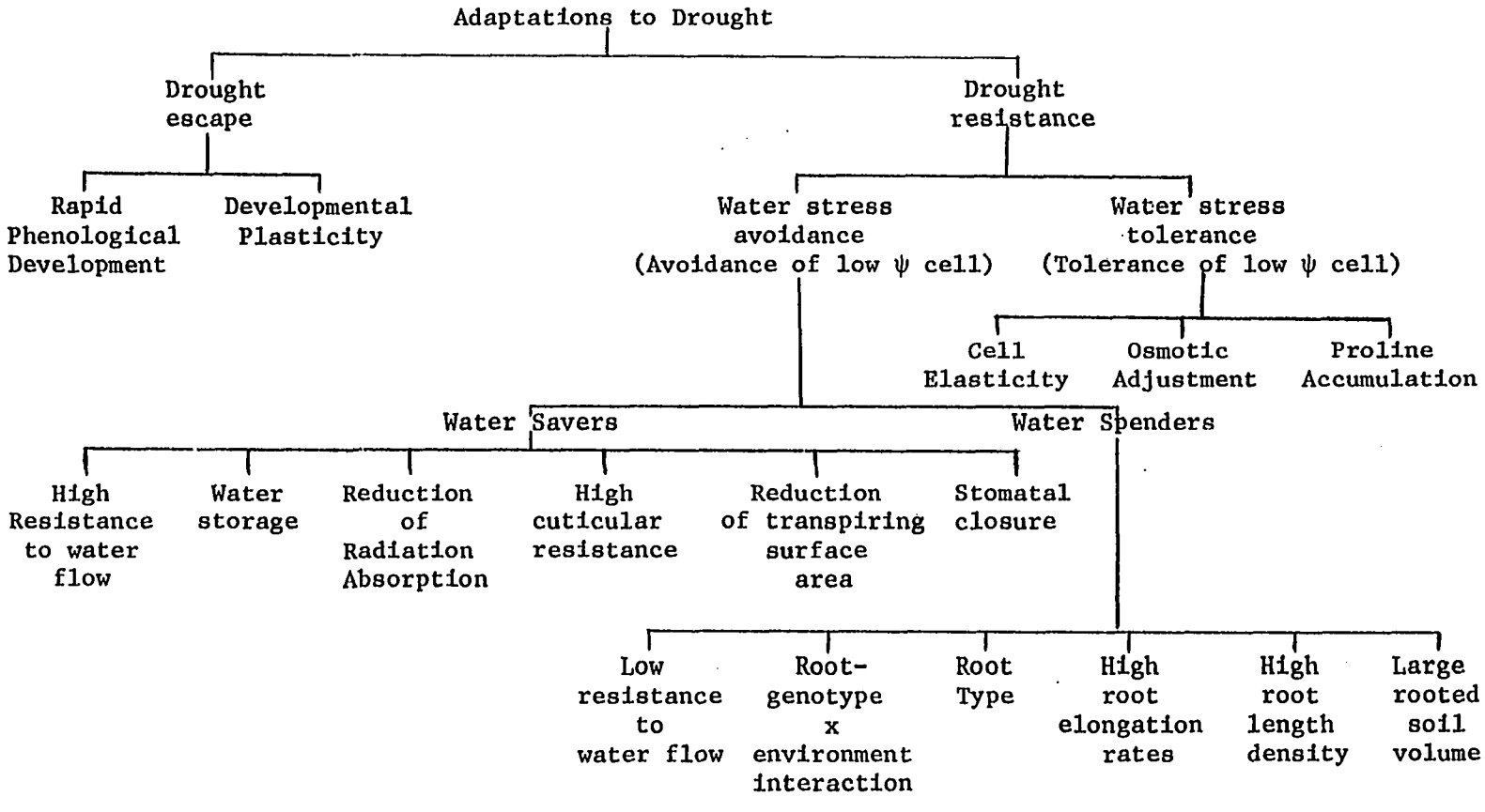


Fig. 1. Principal categories of drought adaptation and some of their components (from Levitt, 1980).

spp.), to avoid the dry summer months in some areas (Derera et al., 1969; Chinoy, 1960). Furthermore, Fischer and Maurer (1978) found that the yield advantage of early maturing wheat and barley (Hordeum vulgare L.) lines increased when the summer drought was more severe. In general, a crop genotype will yield better if its growth characteristics and phenology are precisely adapted to the local ecological conditions. For example, Bunting (1971) found that local African sorghum (Sorghum bicolor (L.) Moench.) varieties headed on or near the average date of the end of the wet season in their particular locality and usually yielded better than more widely adapted varieties. Thus, earliness can be an advantage in areas with a marked, predictable dry season, but would not provide a yield advantage for indeterminate crops grown in areas exposed to periodic or unpredictable drought during critical stages of the growing season (May and Milthorpe, 1962; Blum, 1979).

Developmental plasticity Developmental plasticity is the other drought escape adaptation found in crop plants. In general, developmental plasticity is the modification of the rate, timing, and morphology of plant development, especially reproductive development, by environmental factors, such as the amount of available water. Three types of developmental plasticity are commonly found in crop plants.

The first is the change that occurs in the rate of development or growth as a result of water stress. For instance, mild water stress between floral initiation and anthesis hastens maturity in wheat (Angus and Moncur, 1977). The maturity of cowpeas (Vigna sinensis Endl.) and chickpeas (Cicer arietinum L.) is also hastened or delayed by the timing

of water availability (Sheldrake and Saxena, 1979; Turk et al., 1980). Sorghum, on the other hand, is capable of a kind of reproductive dormancy during drought and will tiller or head after drought is relieved (Martin, 1930). Similarly, when primordia production in barley is slowed by water stress, an accelerated rate of primordia production, after stress is relieved, will often compensate (Nicholls and May, 1963). Even maize, which is not considered as drought resistant as wheat or sorghum, often has an accelerated rate of development after a delay due to water stress (Damptey and Aspinall, 1976). Thus, flexibility in the rate of development can allow crop plants to compensate for some of the effects of drought on reproductive development.

The second type of developmental plasticity is adjustment of reproductive capacity by plants to allow maximum production of viable seeds. Both barley and wheat, for example, have the capability to produce a large number of tillers, but the number of tillers that produce ears is controlled partly by water availability between floral initiation and ear emergence (Begg and Turner, 1976; Jones and Kirby, 1977). In addition, small grain crops also maintain plasticity in the number of spikelets and florets that produce grain until late in reproductive development (Slatyer, 1973; Fischer, 1973). Legumes also demonstrate a great amount of reproductive flexibility because of their indeterminate growth habit. For instance, flower abortion caused by water stress early in flowering can be partly compensated for by retention of more flowers later on (Shaw and Laing, 1966; Turk et al.,

1980). Furthermore, a reduction in the number of pods by water stress can be partly compensated for by an increase in seed size (Momen et al., 1979; Turk et al., 1980). Similarly, when the number of panicles of sorghum, a determinate species, is reduced by drought stress, the number of grains per panicle or grain size may increase if rain comes later in the growing season (Blum, 1973; Bagga et al., 1973).

The third aspect of developmental plasticity is the ability of plants to translocate assimilate accumulated prior to anthesis to developing reproductive structures if current photosynthesis is limited by water stress. For example, wheat translocates a greater percentage of assimilates to the developing grain from the stem, lower leaves, and roots when stressed (Passioura, 1976; Wardlaw, 1967; Hurd and Spratt, 1975). Additionally, Constable and Hearn (1978) showed that soybean (Glycine max (L.) Merr.) cultivars differed in amount of stored assimilate translocated from the stem to developing seeds during drought. In summary, developmental plasticity can allow crop plants to compensate for the effects of drought stress, and the degree of a crop plant's developmental plasticity can, in part, determine its yield when exposed to drought.

Water stress avoidance

Water stress avoidance is prolonged maintenance of relatively high water potential by plants exposed to external water stress (Levitt, 1980). Among native desert plants there are two types of water stress or drought avoiders: (1) water savers, which maintain high water potentials by restricting their rate of water loss, and (2) water

spenders, which maintain high water potentials because of the efficiency and extensiveness of their water uptake and transport systems (Maximov, 1929).

Water saving adaptations Crop plants also demonstrate many of the water saving adaptations of desert plants. For instance, the principal function of stomata in all plants is the regulation of water loss (Begg and Turner, 1976; Turner, 1979). How well stomata regulate water loss, however, is what usually determines a crop's water saving ability (Kramer, 1969; Townley-Smith and Hurd, 1979). For example, one reason 'Pitic 62' durum wheat maintains higher plant water potentials during drought than other cultivars is that Pitic 62's stomata close rapidly as soon as leaf water potential begins to fall (Kaul, 1974; Dedio, 1975). Similarly, stomata of drought avoidant oat (Avena sativa) cultivars open at low light intensities and close at high leaf water potentials (Stocker, 1961). Thus, the responsiveness of stomata to changing plant water status is very important to transpiration regulation. Unfortunately, after a severe water stress, stomata of some plant genotypes do not function normally and remain closed for some time after reestablishment of leaf turgor. Therefore, because increased stomatal resistance also limits CO_2 uptake and fixation, water stress reduces the growth of genotypes, whose stomata open rapidly after turgor is reestablished, to a lesser extent than that of genotypes that open more slowly (Naidu and Bhagyalakshnii, 1967; Glover, 1959). Another aspect of stomatal control of water loss is stomatal density. Low stomatal density is correlated with drought avoidance in blue panicgrass

and barley lines (Dobrenz et al., 1969; Miskin et al., 1972). Additionally, lower stomatal densities have been significantly correlated with higher yield among sorghum genotypes during drought (Liang et al., 1975). Finally, even partial stomatal closure can significantly reduce water loss. Partial stomatal closure in maize may increase the water use efficiency of this crop, because even when stomata are partially closed mesophyll resistance to CO_2 diffusion is much greater than stomatal resistance, and therefore water diffusion would be reduced by a relatively greater amount (Shimishi, 1963; Turner, 1979; Waggoner and Zelitch, 1965).

Even if stomata are very responsive to changes in plant water status, effective control of transpiration can only occur if cuticular resistance is great. For instance, Dube et al. (1975) found that the more drought avoidant of two maize lines had a much greater cuticular resistance than the other. In general, the amount of epicuticular wax deposited on the leaf determines the level of cuticular resistance. Thus, the water use efficiency (Chatterton et al., 1975) and the overall drought avoidance of sorghum genotypes (Ebercon et al., 1977; Blum, 1979) is improved by substantial deposits of epicuticular wax.

Another plant mechanism for reducing water loss during drought is reduction of leaf area. Reducing the leaf area of a crop canopy can reduce the amount of solar radiation intercepted and does reduce the transpiring surface area. Furthermore, crop transpiration is linearly related to leaf area until almost 95% of the incident solar radiation is intercepted (Ritchie, 1974; Turk and Hall, 1980b). In crop species,

such as maize or soybean, inhibition of leaf expansion by water stress during vegetative growth can reduce the final leaf area attained by these crops (Boyer, 1971; Acevedo et al., 1971). Alternately, drought stress can reduce leaf area by hastening senescence of physiologically older leaves (Furuhata and Mousi, 1973; Constable and Hearn, 1978; Turk and Hall, 1980a; Boyer and McPherson, 1975; Begg and Turner, 1976). Reductions in leaf area before complete ground cover, however, also reduce photosynthetic potential and thus, leaf area reductions may also reduce yield in some cases. Additionally, no evidence of cultivar differences in drought induced leaf senescence or inhibition of leaf expansion has been recorded (Turner, 1979).

As mentioned earlier, transpiration from a crop canopy is also partly determined by the total amount of solar radiation absorbed by the canopy. If radiation absorption is reduced, transpiration will also decline because the incident solar radiation provides the energy for water evaporation. Crop plants reduce radiation absorption in several ways. One way is the reorientation of leaves relative to the sun. For instance, water stress causes soybean leaves to invert, exposing their more reflective abaxial surface to the sun (Meyer and Walker, 1981). Similarly, cowpea leaflets become more vertically oriented during water stress (Shackel and Hall, 1979). When vertically oriented cowpea leaves are manually moved and then supported in a horizontal position, a substantial increase in leaflet temperature occurs, indicating that the original vertical orientation does reduce radiation absorption (Shackel and Hall, 1979). Leaf rolling or wilting also reduces radiation

interception. Grass species, such as wheat or sorghum, roll their leaves at high levels of water stress (Blum, 1979; Parker, 1968; Hurd, 1976), whereas, sunflower (Helianthus annus L.) leaves droop or wilt, thus reducing the amount of surface area perpendicular to incident radiation (Rawson, 1979). Furthermore, Rawson (1979) showed that wilted sunflower leaves had 50% of the unstressed photosynthetic rate, decreased heat loads, and improved water use efficiency. Similarly, Hurd (1976) observed that most drought adapted wheat cultivars rolled their leaves and continued to photosynthesize when severely stressed, whereas poorly adapted cultivars did neither.

Another way plants decrease radiation interception is by greater leaf reflectance. Isogenic barley lines with light-green or golden leaves reflect more light than lines with dark-green leaves, and thus, remain cooler (Ferguson, 1974). Wax bloom on sorghum leaves also increases reflectance and reduces water loss (Chatterton et al.,1975; Blum, 1975a; Blum 1975b). Similarly, enlarged white hairs (Woolley, 1964) or increased pubescence on leaves can also increase leaf reflectance (Quarrie and Jones, 1977).

Canopy transpiration is also influenced by soil water availability and the resistance to flow through the plant. Resistance to water flow in the root and between the root and the soil may account for a large portion of the resistance in the soil-plant-air continuum. Root systems that are not extending rapidly into moist soil volumes, or that have high resistances to water flow, will restrict water loss simply because they are not capable of supplying water fast enough to sustain

transpiration at high levels. In areas where crops are grown on a limited supply of soil water, restriction of water use during vegetative growth could be an advantage because leaf area is reduced and more water is available for use during critical reproductive phases (Passioura, 1972). For instance, wheat yield is correlated with water use after anthesis, if the seasonal water supply is limited (Passioura, 1976; Nix and Fitzpatrick, 1969). Similarly, perennial ryegrass (Lolium perenne L.) clones (Troughton, 1974) and maize genotypes (Pallas and Bertrand, 1966) developed leaf water deficits more slowly when grown on stored water if their root systems were less extensive.

A final category of plant adaptations classified by Levitt (1980) as a water saving adaptation is water storage or plant capacitance. The significance of plant capacitance as a mechanism for avoiding low leaf water potentials is probably small because the total water content of most crop species is frequently much less than the amount of water they transpire in one day. Nonetheless, hysteresis in the leaf water potential and evapotranspiration relationship of many crop species indicates that plant capacitance does have some affect on plant water relations (Ritchie, 1973; Stern et al., 1977; Reicosky et al., 1982). Furthermore, water storage is a significant factor in the drought avoidance of pineapple (Amanas comosus (L.) Merr.) partly because its transpiration rates are so low. When pineapple is subjected to drought, water is withdrawn from special nonchlorophyllous tissue in the leaves (Eckern, 1965). Similarly, flax (Linum usitatissimum L.) transfers water from the lower part of the stem to young leaves and stem tissues

during drought (Boyer, 1972).

Water spending adaptations Water savers try to prevent development of low plant water potentials by restricting water loss from aerial portions of the plant, whereas water spenders try to accomplish the same thing by increasing water uptake by the underground portion of the plant. For the most part, a water spender's ability to maintain high water potentials is highly correlated with the extent, pattern, morphology, and growth of the root system. The characteristics of a plant's root system are genetically determined, but can be modified by physical or chemical aspects of the soil environment (Pearson, 1974). Nonetheless, root genotypes differ in their ability to extract water from the soil profile (Sullivan and Blum, 1970). For example, Sullivan and Brun (1975) grafted the shoots of one soybean cultivar onto the rootstocks of four different cultivars. When the grafted plants were planted in the field, they found that the genetically different rootstocks differed in their ability to supply water to the shoot, resulting in lower leaf water potentials, photosynthetic rates and yields for two of the rootstock-scion combinations. Thus, crop species (Weaver, 1926) and genotypes within species (Zobel, 1975; Troughton and Whittington, 1968; Mitchell and Russel, 1971) that possess drastically different root systems should also differ in their water uptake abilities. Once again, however, the drought avoiding value of a particular root system characteristic is not always evident and may depend on the influence of environmental conditions.

The volume of soil penetrated by the root system is one root

characteristic that is generally accepted as being important to drought avoidance (Hurd, 1976). The rooted soil volume is important because along with the soil water content and water holding capacity it determines the amount of water available to the plant at any one time. Generally, in areas where the soil profile is recharged with water between cropping seasons, the larger the soil volume explored by the root system, the better the drought avoidance of the crop (Taylor, 1980a; May and Milthorpe, 1962; Corey and Blake, 1953; Kramer, 1969). Also, because crop plants are usually grown in rows or solid stands, roots of plants from one row usually encounter roots from adjacent rows (Bohm, 1977). Consequently, in most cropping systems, lateral expansion of roots results in only limited increases in the rooted soil volume. Alternately, roots extending downward usually do not encounter other roots and would generally increase the volume of soil exploited by the root system. Thus, plants with deeper root systems should be more drought avoidant. For example, Fehrenbacher and Rust (1956) found that the deeper root development of maize hybrids on certain soils favored higher yields because of increased water availability. Similarly, Burton et al. (1957) found that differences in dry matter production of six grass species during drought were correlated with the extensiveness of their root systems below a depth of 120 cm. Additionally, rice (Oryza sativa L.) cultivars with more roots below 30 cm maintained higher dawn and midday leaf water potentials than shallower rooted cultivars (Steponkus et al., 1980; O'Toole and Chang, 1979). Evidence that rooting depth influences drought avoidance has also been found for

genotypes of wheat (Hurd, 1974; Hurd, 1964), sorghum (Bhan et al., 1973; Jordan and Miller, 1980), and cotton (Gossypium hirsutum L.) (Quisenberry et al., 1981).

Another characteristic of root systems that contributes to water uptake efficiency is root length density, the length of roots in a volume of soil. As soil water potential drops below -0.03 MPa, the hydraulic conductivity of most soils begins to decline rapidly and resistance to water flow through the soil can become the limting factor for water flow through the soil-plant-air continuum (Kramer, 1969; Gardner and Ehlig, 1962). A high root length density reduces the distance water travels through the soil, and therefore lessens the impact of decreasing soil hydraulic conductivity (Williams, 1976). Eavis and Taylor (1979), however, found that, at least for soybeans, root length densities above a certain level had no effect on transpiration rates. Nonetheless, there are many reports that high root length densities of some plant genotypes result in drought avoidance in certain environments. For instance, Aamodt and Johnston (1936) and Hurd (1971) found that drought avoidant wheat cultivars had more profusely branched root systems than drought susceptible cultivars. Similarly, Martin (1930) concluded that part of the reason for sorghum's superior drought avoidance was its high root length density.

Russell (1977) believes that the most important plant characteristic for drought avoidance is the ability of the root system to extend rapidly into unexplored soil volumes. He concluded from his observations of alfalfa (Medicago sativa L.) that the drought avoidance

of this crop resulted partly from its rapid root elongation rates. Obviously, the rate of root extension over time determines the size of the rooted soil volume and the root length density within that volume at any given time. Furthermore, under some conditions root extension of some crop genotypes may be rapid enough to maintain transpiration rates at potential levels, because new supplies of water are becoming available faster than water is being used (Kramer and Coile, 1940). In any case, root elongation rates are important to crop drought avoidance because root elongation determines both the amount of readily available water and the total amount of water available throughout the growing season (Taylor, 1980b).

Characteristics of individual roots within a root system can also have profound effects on the water uptake abilities of plants. For example, older roots are less permeable and may take up less water than younger roots (Hayward et al., 1942). Taylor and Klepper (1973) speculated that the high water uptake efficiency of maize roots deep within the profile resulted from the deeper roots being younger. Root diameter may also have an effect on water uptake ability. Large diameter roots may have a high water uptake ability because of their large surface area per unit length ratio, or lower axial resistance. In any case, O'Toole and Chang (1979) found that the drought avoidance of 35 rice cultivars was positively correlated with mean root diameter. In general, the more drought avoidant upland rice cultivars had thicker roots than lowland cultivars. Lastly, the histological origins of the roots that compose a root system may influence water uptake of the whole

root system (Hurd, 1964). For example, drought avoidant wheat cultivars tended to have more first order (Aamodt and Johnston, 1936) or seminal roots (Hurd and Spratt, 1975) than drought susceptible cultivars.

Water uptake abilities of crop genotypes can also differ because root systems of some plant genotypes grow better under adverse or changing environmental conditions than those of other genotypes. In other words, root system characteristics demonstrate genotype by environment interactions. For example, water stress usually reduces total plant growth, but some genotypes can demonstrate an absolute increase in root growth during extended periods of water stress (Doss et al., 1960; Chang et al., 1972; Clements, 1964; Hsiao and Acevedo, 1974). Furthermore, root genotypes also differ in their ability to grow through soil with water potentials much below -0.03 MPa. Portas and Taylor (1976) found that maize roots could grow better in very dry soil (below -0.6 MPa) than tomato (Lycopersicon esculentum Mill.) roots. Similarly, drought avoidant wheat (Hurd, 1964; Hurd, 1968) and rice (Chang et al., 1972) cultivars have roots that penetrate relatively dry soil volumes more rapidly and extensively than drought susceptible cultivars. Capacity of a root system for regrowth (increasing root length densities) in rewetted soil volumes is also an adaptive advantage for drought avoidance (Russell, 1977).

Finally, under conditions of high evaporative demand, water spenders must also have an efficient water transport system in addition to an extensive collection system (Turner, 1979). Thus, in contrast to water savers, plants that depend on rapid rates of water uptake to

maintain plant water potentials must have relatively low resistances to water flow between soil and plant cells. Unlike other water spending plant adaptations that have been discussed, plant water flow resistance is not solely a root system characteristic. Plant resistance to water flow is also partly determined by axial resistance (resistance within xylem vessels) and resistance to flow between xylem vessels and other plant cells. In many plants, however, resistance to water flow between soil and root xylem (radial resistance) is the principal source of water flow resistance (Boyer, 1971; Newman, 1974). Root radial resistance is determined by both the amount of suberization and root symplasm resistance (Newman, 1976). Blum (1979) has suggested that the greater root respiration of a drought avoidant sorghum cultivar as compared with a nonavoidant cultivar may be related to water transport through the root symplasm. Conversely, axial resistance is dependent on the diameter, number, and continuity of xylem vessels (Taylor, 1980b; Levitt, 1980; Turner, 1979). For instance, when water uptake by wheat is restricted to a limited number of seminal roots, thus increasing axial resistance, water use and leaf water potentials are reduced (Passioura, 1972; Meyer and Alston, 1978). Additionally, Richards and Passioura (1981) found large variations in xylem vessel diameters and water use among wheat genotypes. In general, plant resistances to water flow vary widely among species (Boyer, 1971; Willatt and Taylor, 1978), but differences among genotypes within species have not been explored to any great extent. Indirect measurements of differences in resistance to water flow among maize (Dube et al., 1974) and rice (Steponkus et al.,

1980) genotypes have been reported, but no direct measurements have been made (Turner, 1979).

Water stress tolerance

Water stress or drought tolerance is the ability of plants to survive or lessen the effects of low plant water potentials. Whereas drought avoidance adaptations are largely morphological in nature and are usually expressed on the whole plant or organ level, drought tolerance adaptations tend to be more physiological and cellular by nature. As a result, very few drought tolerance adaptations have been found in nature and their mechanisms are poorly understood. Therefore, this discussion of drought tolerance adaptations of crop plants will be limited to three of the more widely known mechanisms: (1) osmotic adjustment, (2) cell elasticity, and (3) proline accumulation.

Drought tolerance, for the most part, involves maintenance of cell turgor in spite of low plant water potentials. Maintenance of cell turgor is important because many physiological functions in plants are influenced directly or indirectly by cell turgor. Cell enlargement, for one, can only occur if cellular turgor pressure is higher than a threshold value determined by physiological, as well as genetic, factors (Hsiao et al., 1976a; Boyer, 1970). Similarly, stomatal functioning involves changes in turgor pressure of guard cells (Meidner and Mansfield, 1968). Quantitatively, cell turgor pressure or potential is equal to the cell's total water potential minus the osmotic potential. Consequently, lowering osmotic potential will increase turgor at a given water potential, and the ability to maintain turgor pressure at low

tissue water potentials by lowering osmotic potential is an important drought tolerance mechanism in plants (Levitt, 1980).

Osmotic adjustment One way in which plants control osmotic potential is by osmotic adjustment. Osmotic adjustment is the lowering of cellular osmotic potential by the net accumulation of solutes in the vacuole in response to water deficits or salinity (Turner and Jones, 1980). A difference in osmotic potential at the same relative water content between well-watered and water-stressed plants of the same species indicates that osmotic adjustment has occurred. Jones and Turner (1978) allowed two sorghum cultivars to slowly adapt to two levels of water stress in the greenhouse. When the plants were rewatered, plants that were more severely stressed had lower osmotic potentials at all relative water contents than those of plants exposed to the milder water stress. The two sorghum cultivars, however, did not differ in their degree of osmotic adjustment at either level of stress. Similarly, evidence of osmotic adjustment in response to water stress has also been found in rice (Steponkus et al., 1980), sorghum, sunflower, (Turner et al., 1978), buffel grass (Cenchrus ciliaris L.), green panic (Panicum maximum), and spear grass (Heteropogon contortus) (Wilson et al., 1980). Cultivar differences, however, in the degree of osmotic adjustment have not been conclusively proven, although some wheat species are known to differ in their ability to maintain turgor during water stress (Morgan, 1977; Morgan, 1980a; Morgan 1980b). Other factors such as plant age and rapidity of stress development may also influence osmotic adjustment. For instance, sorghum plants in which a

severe water stress develops slowly over several weeks demonstrate osmotic adjustment, whereas well-watered plants stressed quickly over several hours do not (Jones and Turner, 1978). Soybeans, on the other hand, seem to be capable of a kind of diurnal osmotic adjustment (Wenkert et al., 1978). Furthermore, although Turner et al. (1978) and Sionit and Kramer (1977) found no evidence of long-term osmotic adjustment by soybeans, Wenkert (1978) and Boote (K. J. Boote, Univ. of Florida, personal communication, 1981) have indicated that long-term osmotic adjustment can occur during reproduction if environmental conditions are right. Obviously, much work needs to be done in this area, including discerning the principal osmoticum.

Cell elasticity Another plant characteristic that influences both osmotic potential and turgor is cell wall elasticity. If environmental conditions cause a reduction in plant water potentials, plant cells lower their water potentials either by increasing net solute concentration or by concentrating solutes through water loss (Morgan, 1980b). When plant cells lose water at positive turgor pressures, cell wall elasticity determines the change in turgor pressure (Wenkert et al., 1978):

$$\text{Water loss} = dV/VT = dP/E$$

where P is the turgor potential, VT is the cell volume at full turgor, and E is the modulus of elasticity. If E is large, cell elasticity is low and water loss results in a large reduction in turgor. If E is small, cell elasticity is high and the decrease in turgor pressure per unit of water loss is small. In general, small cells are more elastic

and therefore maintain turgor better than larger cells (Turner, 1979; Steudle et al., 1977). Additionally, Wenkert et al. (1978) found that cellular elasticity of immature soybean leaves was greater than that of mature leaves. Jones and Turner (1978), however, found that exposure of sorghum to water stress reduced tissue elasticity by one-half, whereas Elston et al. (1976) reported an increase in tissue elasticity of water stressed field beans. In any case, some plant species seem to differ in their cellular elasticity (Turner, 1974; Wilson, 1967) and cellular elasticity may be an important drought tolerance mechanism.

Proline accumulation If osmotic potential of the vacuole is lowered by osmotic adjustment or by water loss, equilibrium between vacuole and cytoplasm will be maintained either by water loss from the cytoplasm or by net increase in cytoplasmic solute concentration. Because the further concentration of cytoplasmic solutes resulting from water loss would be detrimental to enzyme activity, accumulation of a non-toxic, cytoplasmic osmoticum during water stress would be an advantage to most plants. One plant compound that could act as a cytoplasmic osmoticum is proline (Stewart and Lee, 1974). Accumulation of substantial concentrations of free proline in the cytoplasm of water stressed leaves has been reported for many crop species (Stewart and Hanson, 1980). Apparently, proline accumulation during water stress is caused by a combination of stimulated synthesis, inhibition of oxidation, and inhibited protein synthesis (Stewart and Hanson, 1980). Furthermore, the concentration of proline is always higher in the cytoplasm than in the vacuole of water-stressed leaves (Leigh et al.,

1981; Flowers et al., 1977) and proline is the most stable and least inhibitory amino acid (Palfi et al., 1974). Ford and Wilson (1981) examined four tropical grasses and found that proline concentration increased by as much as 100X during water stress and that the combined concentration of proline and betaine were high enough to balance the osmotic potential of the cytoplasm with that of the vacuole. Moreover, drought tolerant barley genotypes are reported to accumulate higher levels of proline during drought than susceptible genotypes (Singh et al., 1972; 1973). Proline accumulation, however, is strongly correlated with leaf water potential, and reported differences among barley genotypes may only reflect differences in rate of development of water stress (Townley-Smith and Hurd, 1979; Stewart and Hanson, 1980). In any case, substantial evidence exists that proline accumulation is involved in drought tolerance and further study is necessary before its exact role is completely understood.

Screening Crop Genotypes for Drought Resistance

Introduction

Because drought limits world crop production more than any other single factor (Kozlowski, 1968), improved crop drought resistance is a major plant breeding goal. Ideally, crop cultivars should have high yields under optimum rainfall conditions and the best possible yields during drought. Additionally, an ideal crop cultivar would also have wide adaptability and good insect and disease resistance. Unfortunately, these breeding objectives are difficult to achieve,

especially high yields during drought. In order to achieve any breeding objective, plant screening techniques must be developed that are quick, easy, and capable of evaluating a large number of individuals without serious injury (Johnson, 1980). But, because the effects of drought on plants are poorly understood and because few, if any, reliable indices of water stress correlated with yield are available, no outstanding screening techniques for drought resistance exist. Presently, four principal selection strategies are used in breeding for yield improvement in drought prone environments: (1) selection for yield in a non-stress environment, (2) selection for yield in a drought-stressed environment, (3) selection for yield stability, and (4) selection for adaptive characteristics or indices of adaptation.

Selection for yield in a non-stress environment

Most crop yield improvements have resulted from yield selection in an optimum environment. Furthermore, improvement of crop yields in general has usually been accompanied by increases of crop yields in drought-prone environments. Consequently, several research groups have concluded that continued yield improvement in drought-prone environments can best be accomplished by selecting for yield in optimum moisture environments (Arnon, 1975; Mederski and Jeffers, 1973; Laing and Fischer, 1977; Roy and Murty, 1970; Johnson and Frey, 1967). This breeding strategy is based on two assumptions (Hall et al., 1979): (1) optimum conditions allow maximum expression of genetic variation and heritability for yield and (2) yield performance in optimum and stress environments are positively correlated. The yield advantage of sorghum

hybrids over openpollinated cultivars in both optimum and drought-stressed environments is an example of a successful breeding program for which these assumptions are true (Blum, 1979). Similarly, Laing and Fischer (1977) concluded that the higher yields of semidwarf wheat cultivars under drought conditions were probably related to their higher yield potential and not to any specific drought resistance mechanism.

Several critical problems, however, are inherent in this approach to increasing yields in drought-prone environments. First, in order to improve yield under water stress, potential yield of the crop must be raised. Raising the yield plateau of any crop is often a slow and expensive task. Secondly, cultivars with high potential yields are not always high yielding under drought conditions (Hurd, 1968; Johnson et al., 1968; Blum, 1973). Hanson and Nelsen (1980) hypothesized that by selecting for maximum yield in an optimum environment plant breeders may have eliminated or impaired many drought-adaptive features in plants. These features are eliminated because assimilate requirements of these adaptations would have limited maximum assimilate storage in the grain. The last problem with this breeding strategy is that most crops are grown under less than optimum rainfall conditions (Kozlowski, 1968). In fact, for the millions of subsistence farmers in the world, yield in the driest years is more important to their survival than long term yields or potential yields (Hall et al., 1979).

Selection for yield in a drought-stressed environment

Selection for yield under problem conditions is one of the traditional breeding approaches to yield-limiting problems like drought. In practice, yield trials are conducted in the drought-prone target area and in this way the drought stress inherent in the environment exerts the selection pressure. Obviously, selection for yield in a specific or localized environment often precludes wide adaptability of the resulting cultivar, but wide adaptability often means mediocre yields in many environments (Reitz, 1974). For example, in order for a genotype to maximize its yields in a drought-prone area, timing of the genotype's growth and maturity must be precisely adapted to the local rainfall and weather pattern (Bunting, 1971). In Nigeria, local sorghum genotypes consistently produce greater yields in their home environment than more widely adapted cultivars, because their date of heading is closely related to the average date of the end of the wet season in that area (Bunting, 1971). Similarly, Blum (1980) observed that when a sorghum population was submitted to yield selection under drought-conditions in Israel, there was a genetic shift in the population toward earliness in flowering and maturity by about 10 days. Another reason selection for drought resistance should be carried out in a droughty environment is that many drought-adaptive characteristics only influence yield when the plant is exposed to water stress. Therefore, these characteristics will be retained in succeeding breeding generations only if yield is limited by drought (Hanson and Nelsen, 1980; Hurd, 1971).

One problem of selecting for yield in drought-prone areas, however,

is that timing or magnitude of drought stress can vary from year to year. As a result, the relative yield ranking of lines is not the same from one year to the next, and lines that would be eliminated in one year may be accceptable in the next (Blum, 1979). One way to compensate for this problem is to increase the size of the breeding populatcn carried from one generation to the next, thereby exposing more lines to several years of yield testing before they are eliminated or advanced. Another way to overcome the variability of the environment is through use of rainout shelters and irrigation (Johnson, 1980). An additional problem with yield selection in a drought-prone environment is that at reduced yield levels heritabilities for yield and yield determining factors are low and selection for yield may be slower and less efficient (Frey, 1964; Johnson and Frey, 1967; Roy and Murty, 1976). The significance of this problem has yet to be evaluated.

Selection for yield stability

Hall et al. (1979) have suggested that the most reliable selection criterion in breeding for drought resistance is yield stability. Similarly, Blum (1973) and Vidal (1981) advocated use of a relative yield index, the ratio of yield of drought stressed plants to yield at optimum irrigation levels. Use of a relative yield index to evaluate drought resistance is based on the assumption that yield stability and yield potential are genetically independent characteristics and can be individually manipulated in a breeding program. For instance, Marquez (in Lewis and Christiansen, 1981) has suggested selecting for both yield stability and potential yield simultaneously, but in separate parts of a

maize breeding population. After several cycles of selection, the two selected populations would be recombined and the resultant population would have genes for both yield stability and yield potential. Unfortunately, breeding programs using this type of selection strategy have not as yet achieved any substantial increases in crop yields in drought-prone environments. Fischer and Maurer (1978), however, have used yield data of wheat cultivars over a range of water stress levels to analyze the effects of yield potential and other plant characteristics on yield. They concluded that both yield potential and yield under drought conditions were important for evaluation of a genotype's drought resistance.

Selection for adaptive characteristics or indices of adaptation

Even though most of the progress in breeding for drought resistance has resulted from yield selection (Sullivan, 1972), selection for drought adaptive characteristics may offer the best potential for future improvements (Hanson and Nelsen, 1980). In order for this to happen, heritable components of drought resistance must be identified and suitable screening procedures developed. When these problems are solved, transfer of drought resistance characteristics to cultivars with superior yielding ability may become a reality (Blum, 1979).

Currently, two examples of breeding-induced improvement of drought resistance provide evidence that selection for drought adaptive characteristics or indices may be possible. In the first case, a breeding program was started in 1960 to attempt to transfer drought resistance, large kernel size, and heavy bushel weight of the wheat

cultivar 'Pelissier' to the high-yielding cultivar 'Lakota' by backcrossing (Hurd et al., 1972). In order to retain both the drought resistance of Pelissier and the high yield of Lakota, a very large number of lines was tested in early generation yield trials at several locations in the drought-prone Canadian prairies. Meanwhile, Hurd (1964) had developed a glassbox greenhouse technique for evaluating wheat root systems and had discovered that the superior drought resistance of Pelissier was largely the result of its root characteristics (Hurd, 1964; 1968). In the final stages of yield testing the root patterns of Lakota, Pelissier, and three of the highest-yielding Lakota^2 x Pelissier hybrid lines were compared using glass boxes, field coring, and seedling root length in sand. In all cases, the Lakota^2 x Pelissier wheat lines developed by selecting under drought conditions had root systems much larger than that of Lakota and similar in pattern and development to the root system of Pelissier. Thus, drought resistance of crop cultivars can be improved through transfer of drought adaptive characteristics.

In the second example, Wright and Jordan (1970) evaluated a large number of boer lovegrass (Eragrostis curvula Nees.) seedlings from 16 sources by subjecting them to controlled desiccation in a growth chamber. Surviving seedlings were grown for seed, and seed from each plant was planted in four replications and again subjected to growth chamber desiccation. Progeny of each plant were ranked according to percent survival. One selection that had the highest survival ranking was evaluated under rangeland conditions and was found to have superior

drought resistance as evidenced by its greater stand density and seedling drought resistance than that of the commonly-grown check line.

Both of these examples illustrate that drought resistance is heritable and that suitable screening procedures can be developed. However, in neither case was selection carried out for a specific, known, drought adaptive characteristic or index. Instead, selection was based on the plants' overall response to drought. Unfortunately, correlations between anatomical, morphological, or physiological characteristics and crop yield during drought vary widely because of strong interactions between these characteristics and their environments (Johnson, 1980). Thus, these characteristics are difficult to select for, and none of them have proven useful as a reliable indicator of a plant's drought resistance. Two approaches have been suggested for overcoming these problems. First, Hurd (1971, 1974, 1976) contends that extensive testing and careful selection of parental lines should be the basis of breeding for drought resistance. The selected parents should possess as many of the known drought adaptive characteristics, such as an extensive root system, as possible. Only a few different crosses should be made and a large population should be carried through the early generations to permit recombination of as many favorable genes as possible. Also, yield testing under drought-stressed conditions should begin as early as possible and continue until homogeneity is attained. Therefore, in this approach, direct selection for drought adaptive characteristics would occur only in selection of parental lines.

The second approach requires the use of fast and reliable screening

techniques capable of evaluating the large number of individuals usually found in breeding populations (Ebercon et al., 1977; Sullivan and Ross, 1979; O'Toole and Chang, 1979). In the past, most of these screening techniques required too much time or labor, and evaluation of the genetic diversity or the importance to crop yield of many drought adaptive traits or indices was impossible. Now, with new techniques, it is to be hoped that some of the problems with large numbers of individuals, standardization, and correlations with yield can be overcome. For example, Blum (1979) has developed a technique using infrared aerial photography for surveying the comparative drought avoidance of a large number of genotypes within a breeding nursery instantaneously. Genotypes with higher leaf temperatures and therefore lower leaf water potentials show up as a lighter shade of red on the infrared film. Another technique, a visual scoring index (O'Toole and Moya, 1978; O'Toole and Chang, 1979; O'Toole and Cruz, 1980) based on leaf rolling and leaf tip burn is highly correlated with leaf water potential and has been successfully used to select drought avoidant rice genotypes. Similarly, Sullivan and Ross (1979) reported on a technique for measuring heat and desiccation tolerance by evaluating electrolyte leakage from leaf discs. And finally, Jordan et al. (1979) used a hydroponic culture system to evaluate the root characteristics of 30 sorghum genotypes. These four examples are only a few of the many techniques being developed for evaluation and selection of drought adaptive characteristics or indices. At the very least, this

approach will increase our understanding of plant drought resistance and should eventually lead to crop yield increases in drought-prone environments.

PART I. COMPARISON OF GLASSHOUSE AND FIELD TRIALS

INTRODUCTION

Water deficit stress often limits the yields of soybeans (Glycine max (L.) Merr.). Yield reductions can be substantial when water stress occurs during flowering and pod set, because of increased rates of flower and pod abortion. Thus, soybean productivity would increase, if the soybean plant's ability to obtain water during reproduction were improved.

In areas where the soil profile is usually recharged with water each year, enlarging the volume of soil penetrated by a soybean root system will increase the amount of water available to the plant and also should delay or moderate the onset of water stress. For a solitary plant, the rooted soil volume can be increased by either lateral or vertical extension of the root system. But, when soybeans are planted in rows of 100 cm or less, lateral roots from the row soon compete with roots from adjacent rows for water and nutrients (Bohm, 1977). Consequently, in a normal cropping situation increased lateral extension of soybean roots would not provide more water to the plant. Roots extending downward, however, would not encounter other roots and therefore, would be able to obtain water from unexploited soil volumes. The value of a deep root system is also supported by Fehrenbacher and Rust (1956), who have shown that the deeper root development of maize (Zea mays L.) on certain soils favored higher yields because of increased water availability. Thus, improvement of water stress avoidance by soybeans might best be accomplished by a breeding program designed to increase depth of the root system.

Before a breeding program to increase soybean rooting depth can begin, the characteristics necessary to produce a deep root system must be identified. One characteristic that may influence rooting depth is the taproot elongation rate. Plant species, such as alfalfa (Medicago sativa L.), that have rapidly elongating and dominant taproots are usually deeply rooted and drought avoidant (Weaver, 1926). Soybean root systems, however, are usually categorized as weakly taprooted or diffuse. Nonetheless, the rate of elongation of the soybean's taproot does, at least partly, determine maximum depth of the root system, because it is initially the deepest segment. Therefore, a soybean line with a dominant, rapidly elongating taproot may have a deeper root system and better water availability than soybean lines with weak, slow-growing taproots. A preliminary glasshouse study has already indicated that taproot elongation rates of soybean cultivars do differ significantly (Taylor et al., 1978).

Another problem that needs to be solved is development of a standardized screening procedure for evaluating and comparing taproot elongation rates of a large number of soybean genotypes. Presently, there are few efficient screening techniques for root characteristics, because root measurements are generally labor-intensive and quite variable, especially in the field (Hall et al., 1979). As a result, most of the attempts to evaluate root characteristics have been carried out in a glasshouse (Hurd, 1968; MacKey, 1973; Taylor et al., 1978). Unfortunately, evaluating a plant characteristic, especially a root characteristic, in a glasshouse is not necessarily a true indication of

field performance and therefore must be validated by field measurements (Sullivan and Blum, 1970).

With these problems in mind, glasshouse and field experiments were conducted:

1. To standardize and improve the glasshouse method of Taylor et al. (1978) for evaluating taproot elongation rates.
2. To determine whether the modified method provides reproducible results.
3. To determine whether soybean cultivars with widely differing rates of taproot elongation in the glasshouse have different patterns of root growth and water extraction with depth in the field.

MATERIALS AND METHODS

Glasshouse Experiment

The technique used in this study for measuring taproot elongation is a modification of the process used by Taylor et al. (1978) and is similar to the tube-culture technique used by Nilsson (1973). Individual soybean plants were grown in each of 200 clear acrylic plastic tubes (184.5 cm long; 7.0 cm internal diameter) filled with medium-grade horticultural vermiculite in a glasshouse. The tubes were inclined 15° from the vertical and were held in place by four metal racks. Each rack held 50 tubes in two rows of 25 and served as blocks in the experimental design. A trough at the bottom of each rack filled with gravel allowed drainage from the open-ended tubes, but kept the vermiculite in place. A bank of four 40-W fluorescent lights and six 100-W incandescent lights mounted on the top of each rack supplemented daylight and maintained a 15.5 h photoperiod. Furthermore, the racks were insulated with 2.5 cm expanded polystyrene sheets to prevent drastic temperature fluctuations of the root medium and to prevent exposure to direct sunlight.

To begin the evaluation process, two uninnoculated, weighted ($\pm$0.0001g) seeds were planted 3 cm deep in moist vermiculite in each tube. After germination, each tube was thinned to one plant. Plants were watered daily with a modified double strength Hoagland's solution (Epstein, 1972), containing chelated iron (4 mg of $Fe \cdot liter^{-1}$). Because of the inclination of the tubes the taproots, which normally grow

vertically, were forced to grow along the inside surface of the tubes and could be easily seen. A taproot could be distinquished from lateral roots, because it was normally the first root visible and usually was larger in diameter. A record of taproot growth with time was obtained by marking the position of the taproot apex on the outside of the tube with a sequence of colored, wax pencils, three times a week. Taproot depth was measured from seed depth to the position of the apex. Occasionally, the root tip would grow away from the inside surface of the tube and would not be seen for several days. In these instances, data for the days on which the root tip was not visible were calculated by extrapolation from apex positions before and after the missing days. Observations of general plant health and appearance were also made. Plants that germinated slowly or that appeared abnormal or diseased in any way were removed and excluded from the data. When a taproot of any of the 200 plants reached the bottom of a tube, all the plants were removed and the apex positions with time recorded. Shoot measurements of leaf area, dry weight, plant height, and growth stage were also recorded and will be discussed in a later paper.

In 1979, seeds of 137 soybean cultivars were obtained from from the Soybean Germplasm Collection at Urbana, Illinois, and from local sources. In 1980, seed of all cultivars was increased in field plots at Ames, Iowa. The 137 cultivars were almost equally divided among Maturity Groups I, II, and III. All cultivars within a maturity group were evaluated in the same trials and were only compared with other cultivars in the same maturity group. Each planting trial consisted of

four randomized complete blocks with 50 observations or tubes each and examined only cultivars from one maturity group. The 50 tubes within each block or rack were randomly assigned to a maximum of 48 cultivars, plus two plantings of the soybean cultivar 'Wayne', which served as a standard. Cultivars from Maturity Groups I and III were evaluated in two planting trials, whereas the Maturity Group II cultivars were evaluated in three trials. The second trials of the Maturity Groups I and III cultivars and the third trial of the Group II cultivars were conducted using the 1980 seed. All other trials were carried out using the seed obtained in 1979.

The glasshouse experiment was analyzed as a split plot design, with trials as the whole-plots and cultivars within trials as the split-plots. Additionally, the split-plots were arranged in a randomized complete block arrangement with each rack of 50 tubes serving as a block. The three maturity groups were analyzed separately and comparisons among maturity groups were not planned. Also, comparisons between cultivars from different maturity groups are not valid. Because the error mean square did not change significantly when cultivars with missing values were eliminated from the analysis, the experimental error was assumed to have a normal distribution with a common variance and was not seriously disturbed by cultivars with missing values.

Nonetheless, Maturity Groups I and III cultivars with less than six observations total, or Group II cultivars with less than eight observations or less than two observations in each trial, were eliminated from the data analysis. As a result, data from only 105 of

the 137 cultivars were analyzed. Furthermore, cultivar sums of squares were computed after allowing for block effects, and the total degrees of freedom were reduced by the number of missing observations. With these precautions, the analysis of variance should be adequately protected.

Field Experiments

The field experiments consist of three separate experiments. Two preliminary experiments were conducted during 1980 and these experiments will be described and discussed only briefly. The third experiment was conducted during 1981, and this experiment will be examined more extensively.

During the summer of 1980, 40 compartments of the Ames rhizotron (Taylor and Bohm, 1976; Kaspar et al., 1978; Bohm, 1979) were planted with 10 Maturity Group II cultivars, five with fast rates of taproot elongation and five with slow rates, as measured in the glasshouse study, in four randomized complete blocks. Eight innoculated seeds per compartment were planted 5 cm deep on 28 May 1980 and later thinned to two plants on 12 June. Measurements of the deepest visible roots at the acrylic plastic viewing-windows in each compartment were taken three times a week until 15 July. On 15 and 16 July, 27 of the 40 compartments were excavated and the maximum depth of rooting determined. Only 27 of the 40 compartments could be excavated, because structural supports prevented removal of the acrylic plastic viewing windows on the other 13. Data were analyzed using the groups of cultivars selected for fast or slow elongation rates as the two treatments.

During 1980, an experiment was also carried out at the Western Iowa Experimental Farm at Castana, Iowa, on Ida silt loam soil (fine silty, mixed, calcareous, mesic family of Typic Udorthents). Twenty-five soybean cultivars of various maturity groups, 00 to VI, were planted in 75 rows 7.6 m long and 76 cm wide in three randomized complete blocks on 8 May 1980. Twelve of the cultivars had relatively fast glasshouse taproot elongation rates and 12 had relatively slow rates. Wayne was also included for comparison. All the cultivars were selected on the basis of preliminary trials of the glasshouse screening procedure, and all 25 had never been included together in any single glasshouse trial. Thirteen of the 25 cultivars were later included in the three maturity groups evaluated in the glasshouse experiment. Taproot depth was determined during 8 to 11 July 1980 using a modified trench profile method (Bohm, 1979). A trench 2 m deep and 1 m wide was dug across all 75 rows, 1.5 m from the end using a backhoe. Using small hand tools to remove the soil, the taproot of a plant close to the trench wall was followed from the surface until its apex was found and depth below the surface recorded. Three plants per cultivar per block were measured in this way.

In early 1981, 32 plots (2 x 12.2 m) in four randomized complete blocks were established at the Western Iowa Experimental Farm at Castana, Iowa, on Ida silt loam soil. Detailed soil characteristics are published (Sivakumar et al., 1977; Mason et al., 1980). Before planting, the plot area was irrigated with 17 cm of water using a sprinkler irrigation system. Soil levels of phosphorus and potassium

were adequate to maintain optimum growth. Soil preparation consisted of deep chisel plowing, followed by smoothing with a spring tooth harrow. Eight Maturity Group II cultivars, four with slow rates and four with relatively fast rates of taproot elongation were randomly assigned to the plots within each block. Each plot was planted with the assigned cultivar in 6 rows, 25 cm wide and 12.2 m long with an 8 row grain drill on 27 May 1980. On 29 May 1980, chloramben herbicide (Amiben) was applied at the label rate (9.35 liter/ha) with hand sprayers. Additionally, liquid sevin insecticide (22% active ingredients) was applied with hand sprayers at a rate of 1.6 liter/ha on 18 June to control leaf damaging insects. A diclofop methyl herbicide (Hoelon) was also applied at 2.6 liter/ha on 25 June to control grasses. Because of reduced emergence due to soil crusting and insect damage some small sections of rows within plots were replanted between 8 and 12 June. All plots were thinned to 10 plants/m of row or 4.0×10^9 plants/ha by 1 July. Plots and border areas were also hand-weeded several times.

Relative root length density and maximum rooting depth were determined using the core-break method (Bohm, 1979). Four 10 cm diameter soil cores per plot were taken between 20 and 24 July to a depth of 200 cm using a tractor-mounted, hydraulic, soil-coring machine with a 10 cm diameter sample tube. A second sampling of six cores per plot to a depth of 235 cm was taken during the period from 10 to 14 August. All cores during both sampling periods were taken in the rows, directly over a plant. Each core was broken apart by hand at the 50, 100, 150, and 200 cm depths and the relative root length density at

these depths was determined by counting the number of roots visible at the breakage faces. Maximum rooting depth was determined by slicing each core with small hand tools to find the deepest root in the core. Soil moisture content and water use with depth were determined by the neutron scattering method by using a Troxler neutron soil moisture probe and two access tubes per plot. Measurements of soil moisture content were taken at five dates during the growing season (15 and 28 July; 4 and 17 August; 9 September). The neutron soil moisture probe was calibrated with the gravimetric method.

Because of the unusually dry winter and spring preceding the growing season in 1981, the soil profile in the plot area was quite dry before irrigation. Originally, it had been planned to start the growing season with the entire soil profile at field capacity. Unfortunately, because of problems with the irrigation equipment, lack of time, weather, topography of the site, and previous cropping history, the soil profiles of some of the plots were not wetted down to the 250 cm depth, and none were entirely at field capacity. Sivakumar et al. (1977) had found that soybean root growth began to decrease whenever the soil water content of the Ida silt loam soil decreased below 0.16 cm^3/cm^3. Therefore, any plot that had a layer of soil with a water content of less than 0.16 cm^3/cm^3, as measured with the neutron soil moisture probe on 15 July, was excluded from the analysis of variance. Because a total of nine plots was excluded from the data, comparisons between individual cultivars could not be made and the analysis of variance was restricted

to comparisons of the differences between the two groups of cultivars with different glasshouse taproot elongation rates.

RESULTS AND DISCUSSION

Glasshouse Experiment

Cultivar means for rate of taproot elongation, as measured in the glasshouse study, are listed in Table 1. Maturity group averages for taproot elongation rate ranged from 4.65 $cm \cdot day^{-1}$ for Group I to 3.45 $cm \cdot day^{-1}$ for Group II. Part of the difference in the maturity group averages resulted from differences in glasshouse conditions during the trials. For example, data collected during trials in early winter probably had slower taproot elongation rates than early-summer trials because of decreased solar radiation, shorter natural daylength, and slightly cooler glasshouse temperatures. Furthermore, Wayne, which was included in all trials, had trial means that were equal to or slightly less than the three maturity group means, indicating that maturity group means were nearly equal to each other within an environment. Taylor et al. (1978) also found that trial averages for the taproot elongation rate differed, even when the same cultivars were used in both trials. Additionally, Stone and Taylor (1982) found that rooting medium temperature strongly influences taproot elongation. Therefore, the maturity group differences in taproot elongation rate are probably due to differences in the glasshouse conditions during their respective trials.

The cultivar means within maturity groups had ranges of 1.20, 1.25, and 1.31 $cm \cdot day^{-1}$ for Groups I, II, and III, respectively. The error variance of Group II cultivars however, was less than that of the other

Table 1. Mean taproot elongation rates of greenhouse-grown soybean cultivars

MATURITY GROUP I			MATURITY GROUP II		
Cultivar	Mean taproot elongation rate ($cm.day^{-1}$)	(observations) n	Cultivar	Mean taproot elongation rate ($cm.day^{-1}$)	(observations) n
Chippewa 64	5.29	(8)	Aksarben	4.28	(8)
Chippewa	5.26	(7)	Magna	4.05	(11)
Rampage	5.18	(7)	Manchu Madison	3.98	(9)
A-100	5.11	(8)	Wells	3.86	(8)
Vinton	5.10	(8)	Hawkeye 63	3.85	(11)
Harly	5.08	(7)	Mudken	3.79	(10)
Wirth	5.06	(8)	Hawkeye	3.78	(10)
Manchu Montreal	5.06	(6)	Madison	3.76	(11)
Elton	5.00	(8)	Beeson	3.67	(10)
Medium Green	4.99	(6)	Wea	3.66	(8)
Harlon	4.98	(6)	Harwood	3.65	(10)
Norsoy	4.86	(8)	Manchukota	3.61	(10)
Renville	4.82	(8)	Henry	3.60	(11)
Black Hawk	4.79	(6)	Linman 533	3.59	(8)
Cayuga	4.77	(6)	Black Eyebrow	3.52	(9)
Disoy	4.70	(7)	Sloan	3.52	(10)
Hark	4.69	(8)	Seneca	3.50	(9)
Dun	4.66	(7)	Wayne	3.49	(16)
Monroe	4.59	(8)	Richland	3.49	(11)
Wayne	4.58	(14)	Waseda	3.48	(12)
Pridesoy	4.50	(8)	Harcor	3.44	(11)
Tortoise Egg	4.50	(6)	Harosoy 63	3.43	(10)
Giant Green	4.48	(8)	Marion	3.41	(12)
Steele	4.46	(7)	Kanro	3.40	(10)
Hodgson	4.42	(7)	Harosoy	3.39	(11)
Bombay	4.37	(6)	Kanum	3.37	(10)
Ottawa	4.36	(8)	Bansei	3.34	(11)
Blackeye	4.33	(6)	Lindarin	3.27	(10)
Kagon	4.31	(6)	Amsoy 71	3.22	(11)
Earlyana	4.27	(8)	Vickery	3.21	(8)
Burwell	4.27	(7)	Korean	3.15	(9)
Mandarin 507	4.23	(7)	Yellow Marvel	3.13	(10)
Hodgson 78	4.22	(8)	Corsoy	3.12	(10)
Hoosier	4.22	(6)	Goku	3.12	(9)
Habaro	4.19	(8)	Amsoy	3.03	(11)
OAC 211	4.13	(8)			
Mendota	4.09	(6)			
Group Avg.	4.65		Group Avg.	3.49	
Error: $s^2 = 0.1247$, df = 224			Error: $s^2 = 0.0784$, df = 310		

MATURITY GROUP III		
Cultivar	Mean taproot elongation rate (observations)	
	$cm \cdot day^{-1}$	n
Columbia	4.82	(7)
Adelphia	4.61	(7)
Woodworth	4.58	(8)
Cloud	4.54	(6)
Pennsoy	4.53	(6)
Adams	4.52	(7)
Mingo	4.52	(6)
Calland	4.51	(8)
Little Wonder	4.43	(7)
Slingto	4.42	(8)
Bavender Spec. B	4.38	(7)
Kim	4.29	(6)
Verde	4.27	(6)
Bavender Spec. A	4.27	(7)
Mansoy	4.25	(7)
Ford	4.24	(7)
Ross	4.23	(7)
Elf	4.20	(8)
Williams	4.19	(8)
Illni	4.18	(6)
Ilsoy	4.16	(7)
Fuji	4.14	(7)
Osaya	4.14	(7)
Viking	4.13	(6)
Chestnut	4.12	(6)
Wayne	4.07	(16)
Dunfield	4.07	(7)
Manchu	4.04	(7)
Guelph	4.04	(8)
Mendel	4.00	(8)
Oakland	3.95	(6)
Chusei	3.83	(6)
Jogun Ames	3.82	(7)
Cumberland	3.81	(8)
Wing Jet	3.51	(8)
Group Avg.	4.21	
Error: $s^2 = 0.1098$, df = 210		

two groups. In any case, the mean taproot elongation rates of cultivars within a maturity group differed at the .01 level of significance for all three groups. Not surprisingly, cultivars that were closely related genetically, such as 'Amsoy' and 'Amsoy 71,' did not differ significantly. On the other hand, the measured difference in actual taproot length of the two extreme Group II cultivars, Amsoy and 'Aksarben', averaged 46 cm over the three trials and was highly significant. Taylor et al. (1978) and Stone and Taylor (1982) also found significant differences in the rate of taproot elongation among soybean cultivars. Although Taylor et al. (1978) used soil instead of vermiculite, and calculated taproot elongation rate using regression analysis, the rates they obtained fall within the range of rates measured in this experiment.

The trial by cultivar interaction was significant at the .01 level for all three maturity groups. The significant trial by cultivar interaction indicates that at least some of the cultivars had different taproot elongation rates relative to the group average from one trial to the next. Examination of the analysis of variance, however, showed that the mean squares for cultivars were three to six times larger than the mean squares for the trial by cultivar interaction for each of the three maturity groups. This large difference in mean squares indicates that the effect of interaction on cultivar means was small compared to the cultivar differences. Also, only a few cultivars in each maturity group had significant interactions. Two trials of the Group II cultivars used seed from the same source and when these trials were analyzed

separately, no significant trial by cultivar interaction was found. The lack of a significant interaction for these two trials seems to indicate that the trial by cultivar interaction may be partly due to seed quality or vigor differences. For example, Burris (1973) has shown that seed size and seed maturation influence soybean seedling root and shoot dry weight at seven days after imbibition. Thus, the small variation of the relative response of some cultivars from trial to trial does not present a major problem for the use of this method as a screening process in a breeding program, especially, if differences in seed quality among cultivars are minimized by producing seed in a common environment (Fehr and Probst, 1971).

Field Experiments

The two field studies conducted during 1980 will be discussed only briefly. In the rhizotron study measurements of roots observed at the acrylic plastic viewing-panels did not reveal any significant differences between the group of soybean cultivars selected for fast rates of taproot elongation and those selected for slow rates of taproot growth. When the acrylic panels were removed and the soil excavated from most of the compartments, the cultivars selected in the glasshouse for fast taproot elongation rates had a maximum rooting depth that was 10 cm deeper ($P < .05$) than that of slow taproot elongators. No attempt was made to determine whether the deepest roots observed were taproots. Additionally, the rhizotron can only approximate field conditions; thus, these results may not reflect the response of a

soybean root system under field conditions. For example, the maximum lateral extension of roots in a rhizotron compartment is only 20 cm and this may have affected the maximum depth attained by the root systems. Nonetheless, the results of this study do support the hypothesis that cultivars with more rapidly elongating taproots, as measured in the glasshouse procedure, will produce deeper root systems.

No significant differences in taproot length were found among the 25 soybean cultivars in the field study at Castana, Iowa during 1980. The modified trench profile method used in this study was not very suitable for evaluating the large number of cultivars that were planted, because of the long time required to obtain each sample. As a result, taproot lengths of only three plants per replication were measured and experimental error was quite large. In fact, experimental error was so large that cultivar differences in taproot length in the field would have had to have been larger than the differences measured in the glasshouse in order to be significant. Thus, the lack of significant differences among cultivars in the field was not surprising considering the normal variability of the field environment.

Observations during these measurements, however, did provide valuable information. First, at least in the Ida silt loam soil, taproots do extend deep into the soil profile, in one case as deep as 160 cm at 63 days after planting. Borst and Thatcher (1931) reported that taproots penetrated to 152 cm under favorable conditions. Secondly, a compacted layer 2-3 cm thick was found at about 18 cm below the surface. The compacted layer often forced taproots to grow

horizontally for as far as 40 cm before a weakness or hole in the compacted layer allowed them to grow downward again. In other cases, the apex of the taproot was damaged during passage through the compacted layer and stopped growing soon afterward. The effect of this compacted layer on the maximum depth attained by the taproot or the root system in general is unknown, but most likely would reduce it. Deep chisel plowing was used to remove this compacted layer before the 1981 experiment. A third observation of interest was the tendency of taproots, and roots in general, to follow vertically oriented insect or worm burrows and root channels left by the previous year's roots. And finally, cultivars of some maturity groups grew poorly and all maturity groups were at different stages of development during sampling. Therefore, only Group II cultivars were used in the 1981 field experiment.

The field experiment at Castana during 1981 provided more conclusive information than the previous studies. Data from the first root sampling period, between 54 and 58 days after planting, are listed in Table 2. A full canopy had developed in all the plots by this time and all cultivars were well into flowering (R2 and R3; Fehr and Caviness, 1977). In general, the four cultivars that had slow rates of taproot elongation had greater relative root length densities at the 50 cm depth and lesser densities at the 100 and 150 cm depth than cultivars selected for fast taproot elongation rates. Differences in relative root length densities between the fast and the slow group, however, were significant only at the 150 cm depth. Maximum rooting depths of

cultivars selected in the glasshouse for fast taproot elongation rates averaged 9.0 cm deeper than the group of slow elongating cultivars ($P < .10$). In the previous year's experiment at Castana, taproot depths of 94 and 122 cm were measured for Amsoy 71 and Hawkeye 63, respectively, on 19 July, about 62 days after planting, whereas during the first sampling period in 1981, the rooting depths of Amsoy 71 and Hawkeye 63 were 134 and 142 cm.

Table 3 contains data from the second root sampling period between 75 to 79 days after planting. All of the cultivars were filling seeds at this time (R5) and stem elongation had terminated. The trends in root length density were the same as that of the first sampling period. The cultivars with slower taproot elongation rates had greater relative root length densities at the 50 cm depth, whereas the fast elongating group had greater root length densities at the 100, 150, and 200 cm depths. The differences, however, were not statistically significant. During sampling, many roots were found below 200 cm and one live root was found at a depth of 230 cm below the surface. Previously, Willatt and Taylor (1978) had found roots as deep as 225 cm at Castana, but only at 129 days after planting. The average maximum rooting depth of the fast group of cultivars was 177.6 cm, which was 9.4 cm deeper than that of the slow group. But, this result was not significantly different, even at the 0.10 level.

Using the rooting depth data for calculation, cultivars selected for fast taproot elongation increased their rooting depth by an average of 2.3 $cm \cdot day^{-1}$. Allmaras et al. (1975) measured a 1.7 $cm \cdot day^{-1}$ rate of

Table 2. Cultivar and group means for relative root length density and maximum rooting depth obtained from soil cores at Castana, Iowa, 20 to 24 July, 1981

	Relative root length density (root counts)				Maximum rooting depth (cm)
	50	100	150	200	
	depth (cm)				
Cultivars with slow taproot elongation rates					
Yellow Marvel	4.7	3.3	0.3	0.0	130.6
Vickery	4.8	1.2	0.0	0.0	111.7
Kanum	4.6	1.9	0.2	0.0	128.8
Amsoy 71	4.6	5.4	0.1	0.0	134.1
Slow group average	4.7	2.6	0.2*	0.0	126.3***
Cultivars with fast taproot elongation rates					
Magna	4.2	2.3	0.4	0.0	132.7
Aksarben	2.6	2.8	0.4	0.0	128.1
Hawkeye 63	4.1	2.8	0.5	0.0	142.0
Manchu, Madison	6.6	3.7	0.2	0.0	138.3
Fast group average	4.6	2.8	0.4*	0.0	135.3***

*,*** Values are significantly different at .05 and .10 levels, respectively.

soybean rooting depth increase on a heavier soil in Minnesota. These rates are substantially less than taproot elongation rates measured in the glasshouse. But, the field rates would be expected to be less than glasshouse elongation rates because the Ida soil at Castana has a much greater bulk density than vermiculite, and because the soil temperatures were lower than those of the vermiculite in the glasshouse. Stone and Taylor (1982) have shown that taproot elongation decreases as rooting-medium temperature decreases below 29 C.

Soil water contents as a function of depth for five dates between 15 July and 9 September are presented in Figure 2 for the groups of cultivars with fast and slow taproot elongation rates, respectively. For both groups of cultivars the zone of maximum water extraction became deeper with time. Rainfall during late August and early September rewet the upper 30 cm of the soil profile. In general, the water content curves show more water uptake by the fast taproot elongators at depths below 120 cm and less above than for the slow elongators. Total measured water use among all eight cultivars did not differ significantly.

The percentage of measured water use with depth for a given time period was calculated by determining the change in water content at a given depth and dividing by the total measured water use at the seven depths. These data for three time periods arepresented in Table 4. In general, the group of cultivars selected for fast taproot elongation rates in the glasshouse obtained a greater percentage of their water from deeper in the profile than did cultivars that had slower taproot

Table 3. Cultivar and group means for relative root length density and maximum rooting depth obtained from soil cores at Castana, Iowa, 10 to 14 August, 1981

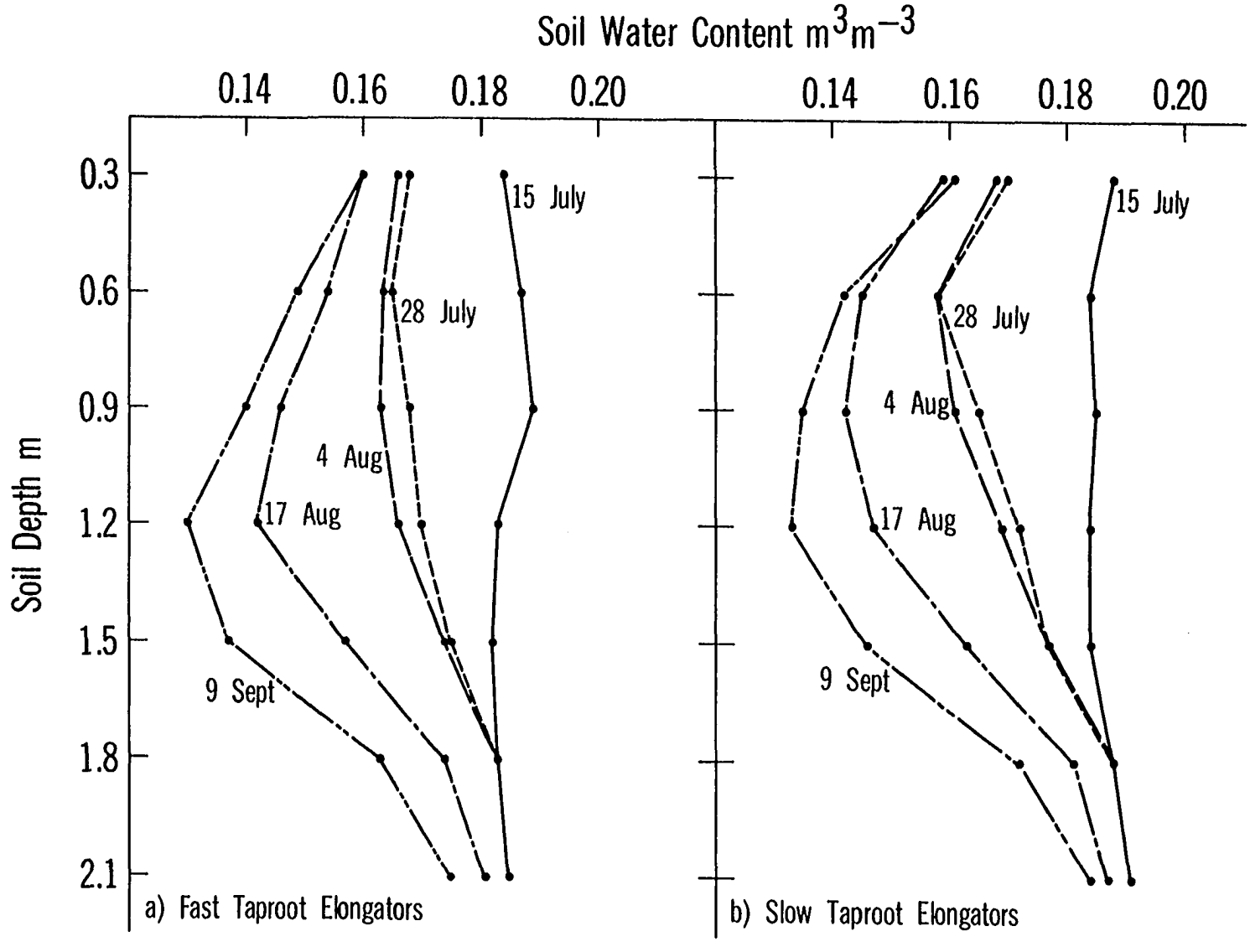
	Relative root length density (root counts)				Maximum rooting depth (cm)
	50	100	150	200	
	depth (cm)				
Cultivars with slow taproot elongation rates					
Yellow Marvel	7.0	5.0	1.4	0.1	161.6
Vickery	5.2	4.4	2.8	0.0	178.0
Kanum	4.0	5.8	1.6	0.1	169.5
Amsoy 71	4.6	2.5	1.2	0.0	158.7
Slow group average	5.2	4.4	1.8	0.1	167.0
Cultivars with fast taproot elongation rates					
Magna	4.3	5.5	2.9	0.4	186.1
Aksarben	5.2	4.7	1.9	0.3	177.5
Hawkeye 63	4.2	4.1	1.5	0.1	169.7
Manchu, Madison	6.1	6.8	1.7	0.2	176.9
Fast group average	5.0	5.3	2.0	0.3	177.6

elongation rates. For example, for the period between 49 and 69 days after planting the cultivars with faster rates obtained a significantly greater percentage of their water from the 120 cm level than the slow group did. Furthermore, although not significant, the slow group had greater values at the 30 and 60 cm levels, whereas the fast group had the greatest values at 90 and 150. No water use at the 180 and 210 cm levels was recorded during this period, because roots had not extended to these depths by 69 days after planting.

A similar pattern of water extraction was found for both the periods from 49 to 82 days after planting and from 69 to 105 days after planting. Between 49 and 82 days after planting, the slow cultivar group had significantly greater percentages of water use at the 30 and 60 cm levels and significantly lesser percentages at 120 and 150 cm. During the period between 69 and 105 days after planting, the fast cultivar group obtained a significantly greater percentage of its water from 150 cm level and a significantly lesser percentage of its water from the 90 cm level than the slow cultivar group did.

The water use data for 69 to 105 days after planting also show the increasing importance of successively deeper soil levels as the growing season progresses. For example, more than 60% of the total water use during this period, which includes the reproductive stages of development, was obtained below the 105 cm depth, whereas during the period from 49 to 69 days after planting more than 70% of the measured water uptake came from above the 105 cm level. One reason, a greater percentage of water was obtained from deeper in the profile latter in

Fig. 2. Soil water contents as a function of soil depth for (a) soybean cultivars with relatively fast taproot elongation rates and (b) soybean cultivars with relatively slow taproot elongation rates


Soil Water Content m^3m^{-3}
0.14
0.16
0.18
0.20
0.14
0.16
0.18
0.20
Soil Depth m
0.3
0.6
0.9
1.2
1.5
1.8
2.1
15 July
28 July
4 Aug
17 Aug
9 Sept
a) Fast Taproot Elongators
15 July
28 July
4 Aug
17 Aug
9 Sept
b) Slow Taproot Elongators

the season was because most of the water in the upper part of the profile was gone. Thus, soybean root systems that normally are more extensive in the deeper soil layers, should be better able to obtain water later in the growing season, especially in dry years.

Table 4. Group means of soybean cultivars selected for either fast or slow taproot elongation rates, for the percentage of the total measured water use with depth during specified time periods

Relative rate of taproot elongation	Percentage of total measured water use with depth (cm)						
	30	60	90	120	150	180	210
			Between 49 and 69 days after planting				
Fast	15	26	31	19 *	9	--	--
Slow	20	29	27	16	8	--	--
			Between 49 and 82 days after planting				
Fast	14 *	18 *	24	22 **	13 *	6	3
Slow	16	21	24	20	11	5	4
			Between 69 and 105 days after planting				
Fast	6	10	16 **	24	25 **	13	6
Slow	6	11	20	27	22	10	4

*,** Values are significantly different at .05 and .01 levels, respectively.

CONCLUSIONS

The glasshouse method for measuring soybean taproot elongation does produce consistent results and could be used as a screening process. Data from several field experiments are compatible with the hypothesis that soybean cultivars with widely differing taproot elongation rates, as measured by the glasshouse method, do have different patterns of root growth and water extraction with depth. Therefore, this screening procedure could be used to select parental lines with rapidly elongating taproots for soybean breeding programs attempting to improve drought avoidance, as suggested by Hurd (1976).

PART II. FACTORS INFLUENCING RATE OF TAPROOT ELONGATION

INTRODUCTION

Soybean (Glycine max (L.) Merr.) cultivars with rapidly elongating taproots have deep root systems and obtain a large percentage of their water from deep in the soil profile (Kaspar et al., 1982). A glasshouse procedure for measuring taproot elongation rate (Taylor et al., 1978; Kaspar et al., 1982) may allow selection of parental lines with rapidly growing taproots for breeding programs designed to improve soybean drought avoidance. Therefore, understanding the plant characteristics or cultural practices that influence or correlate with taproot elongation is important to the successful use of this procedure and may help to increase the capacity of the system for evaluating soybean lines.

Kaspar et al. (1982) determined taproot elongation rate by dividing taproot length by the number of days required for at least one taproot to grow 177 cm (bottom of tube). Time required to measure the elongation rate might be reduced and the capactiy of the system increased, if taproot elongation could be measured over a pre-established, shorter time interval. Another possibility for enhancing the capability for screening soybean lines would be to use an initial screening, based on some easily measured characteristic closely correlated with taproot elongation to reduce the number of lines requiring extensive evaluation. To evaluate both these possibilities, data collected during the glasshouse experiment of Kaspar et al. (1982) were used to determine the correlations among taproot elongation rate, shoot growth characteristics, seed weight, and elongation rates over

short time intervals.

Another problem limiting applicability of this or any screening or measurement procedure is size of the experimental error. Therefore, it is important to know the effect of planting depth, seed quality, seed source, and seedling damage on the variability of taproot elongation rates. For example, Burris et al. (1971) found that radicle length of soybeans at 7 days after imbibition decreased with decreasing seed size and that smaller seed may result in decreased yield. Similarly, Fehr and Probst (1971) found that yield, maturity, height, lodging, and harvested seed size of soybean plants grown from seed obtained from 14 diverse locations differed significantly. Lastly, even in the glasshouse, young soybean seedlings are often damaged by disease, insects, or mechanical force. Plant damage at early plant growth stages can cause soybean yield reductions in field-grown plants (Weber and Caldwell, 1966), but the effect of seedling damage on taproot growth is unknown. Therefore, three experiments were conducted to determine the effects of planting depth, seed source, seed weight, and seedling damage on taproot elongation.

MATERIALS AND METHODS

General Procedure

Four experiments were conducted in a glasshouse at Ames, Iowa, during 1980 and 1981. Each of the four experiments utilized the same cultural practices and methodology for measuring taproot elongation rate as described by Kaspar et al. (1982). Briefly, individual soybean plants were grown in each of 200 clear acrylic plastic tubes (185 cm length; 7.0 cm internal diameter) filled with vermiculite. The tubes were inclined at 15° from the vertical, so that the taproots would grow along the inside surface of the tubes. Initially, two weighed seeds of a randomly assigned cultivar or treatment were planted 3 cm deep in each tube. After emergence, each tube was thinned to one plant. Plants that were diseased, damaged, or emerged slowly were also removed. All plants were supplied with supplemental lighting and were watered daily with a double-strength modified Hoagland's solution. Tri-weekly measurements of taproot elongation were made by marking the progress of taproots on the outside of tubes with a sequence of colored, wax pencils. When one plant in any of the 200 tubes reached the bottom (28 to 48 days after planting; 177 cm from planting depth) all plants were removed for top growth measurements. Taproot elongation rate was determined by measuring the distance between the taproot apex and seed depth and dividing it by the number of days in the trial.

Correlation Experiment

Correlation coefficients among taproot elongation rates, leaf areas, shoot dry weights, plant heights, seed weights, and elongation rates during short time intervals were determined using data gathered during glasshouse experiments described by Kaspar et al. (1982). One hundred five soybean cultivars from Maturity Groups I, II, and III were evaluated in seven planting trials. Each planting trial evaluated cultivars from only one maturity group. At the conclusion of each trial, plants were cut off at the surface of the vermiculite. Stage of development (Fehr and Caviness, 1977) and plant height were recorded. Leaf area was determined to $\pm$ 1% using a Li-Cor (LI-3000) leaf area meter with the transparent-belt conveyor accessory. Shoot dry weight was determined by drying at 60 C for 48 h in a forced-air-flow drying oven and weighing on an analytical balance to $\pm$ 0.001g. Seed weight was determined by weighing to $\pm$ 0.0001g on an analytical balance.

Seed Weight Experiment

Four soybean cultivars, 'Magna', 'Manchu Madison', 'Kanro', and 'Vickery' were selected for the seed weight part of this study. Magna and Manchu Madison have much faster taproot elongation rates than Vickery and Kanro (Kaspar et al., 1982). Furthermore, Magna and Kanro are generally considered 'large-seeded' types (280 and 286 mg/seed, respectively), whereas Manchu Madison and Vickery have seed of average size and weight (151 and 159 mg/seed, respectively). Seed for this experiment was obtained from 1980 seed increase plots at Ames, Iowa.

From both the Magna and Kanro seed lots, 32 seeds that weighed between 320 and 340 mg/seed and 32 seeds that weighed between 220 and 240 mg/seed were selected and weighed to $\pm$ 0.0001 using an analytical balance. Similarly, 32 seeds that weighed between 190 and 210 mg/seed and 32 that weighed between 110 and 90 mg/seed were selected from the Manchu Madison and Vickery seed lots. The two seed weight categories for each cultivar will be referred to as the'heavy' and 'light' seed weights. In all, there were four cultivars and two weight categories per cultivar or eight treatment combinations. A 2 x 4 factorial experiment was arranged in a randomized complete block design with eight blocks. Taproot elongation was measured over 35 days.

Seed Source Experiment

Seventy-two tubes were divided into eight randomized complete blocks and planted with seed of the soybean cultivar 'Wayne' from nine different seedlot combinations of source, year of production, and cultural treatment. Planned individual degree of freedom comparisons were utilized in the data analysis. Plants were grown for 35 days after planting. Shoot growth measurements also were made at the conclusion of the experiment.

Depth of Planting Experiment

Four soybean cultivars, Magna, Kanro, Manchu Madison, and Vickery were planted at three depths, 3, 6, and 9 cm, to determine whether depth of planting affects taproot elongation rate. The experiment was

designed as a 3 x 4 factorial combination arranged in eight randomized complete blocks. Wayne was also planted in each block at a depth of 3.0 cm as a standard. Measurements of taproot elongation with time and shoot growth were made as in the other experiments. The planting depth trial lasted 34 days. Seed used in this experiment was obtained from 1980 Ames seed increase plots, and only seed that weighed within 30 mg of the average seed weight was used.

Seedling Damage Experiment

Five seedling damage treatments and a control were applied to four soybean cultivars, Magna, Kanro, Manchu Madison, and 'Amsoy 71' in a 6 x 4 factorial experiment arranged in a randomized complete block design with eight blocks. As in the other experiment, seed was obtained from the 1980 Ames seed increase plots. Also, Magna and Manchu Madison had faster taproot elongation rates than Amsoy 71 and Kanro. Seed of Amsoy 71 is considered to be average size and weight (173 mg/seed). Only seeds within 30 mg of the average seed weight were used. Seedling damage treatments, which consisted of removal of various plant parts, were applied at 8 days after planting at plant growth stage VC (Fehr and Caviness, 1977). Measurements of taproot elongation with time and shoot growth measurements were taken as described previously. The seedling damage experiment lasted 40 days.

RESULTS AND DISCUSSION

Correlation Experiment

MacKey (1973) has reported that a tall wheat plant or cultivar (Triticum spp.) tends to develop a deeper root system than a shorter plant. Similarly, soybean plant height was highly correlated with rooting depth in the field (Mayaki et al., 1976). Taylor et al. (1978) found that soybean shoot dry weight and seed weight were positively correlated (r=.55 and .18; respectively) to glasshouse taproot elongation. Conversely, the taproot length of peas (Pisum sativum L.) was not significantly correlated with either shoot height or dry weight among 29 genotypes (Ali-Khan and Snoad, 1977).

Table 5 contains correlation coefficients, based upon cultivar means, among the taproot elongation rates, seed weights, and shoot growth measurements of 105 glasshouse-grown soybean cultivars. Average cultivar height was positively correlated with cultivar taproot elongation rate, whereas seed weight, shoot dry weight, and leaf area were not. The tallest cultivars, however, did not always have the fastest taproot elongation rates. For example, only 6 of the 15 tallest Group II cultivars were also among the 15 fastest taproot elongators. Therefore, even though tall soybean cultivars tended to have faster taproot elongation rates than shorter cultivars, plant height probably could not be used as a preliminary screening criterion to find cultivars with rapid taproot elongation rates. Similarily, Taylor et al. (1978) concluded that much of the variation among soybean cultivars' taproot

elongation rates was associated with factors other than shoot growth.

In many breeding or screening programs, the length of time required to evaluate individuals for a particular trait is often a factor limiting the number of genotypes that can be evaluated. Therefore, shortening the time needed to measure taproot elongation rate is one way to increase the number of individuals that can be screened using the glasshouse procedure. Taylor et al. (1978) measured taproot length at irregular 1 to 4 day intervals and determined the rate of elongation from the linear regression of taproot length on time over 26 and 27 day periods. On the other hand, Kaspar et al. (1982) determined taproot elongation rates by dividing the taproot length of each plant by the number of days required for the first taproot in a planting to elongate 177 cm (28 to 48 days). In both experiments, cultivar elongation rates differed significantly.

Table 6 contains the correlation coefficients between the standard taproot elongation rate, which is the rate determined by the method of Kaspar et al. (1982) and elongation rates for shorter time intervals for the same cultivars during the same trial. Not surprisingly, all of the rates based on shorter time intervals were significantly correlated with the standard elongation rate, and the rate from 0 to 28 days after planting had the strongest relationship.

Data for the Maturity Group II cultivars (Kaspar et al., 1982) were examined to compare the relative ranking of cultivars for the standard taproot elongation rate, the 0 to 21 day rate, and the 0 to 28 day rate. The range of cultivar means and cultivars ranking in the upper 15% of

Table 5. Correlation coefficients between soybean mean cultivar taproot elongation rates and cultivar means for seed weight, and shoot growth measurements, along with their means and ranges of values (n = 105).

	Correlation coefficient with elongation rate	Mean	Range
Elongation rate	--	4.13 $cm.day^{-1}$	3.00-5.29 $cm.day^{-1}$
Seed weight	-.02	0.200 g	0.122-0.329 g
Plant height	.45**	52 cm	34-76 cm
Shoot dry weight	.10	6.92 g	4.39-11.61 g
Leaf area	-.02	1360 cm^2	885-3669 cm^2

**Significant at the .01 level.

the data range were virtually the same for all three measurements intervals. The standard elongation rate, however, had an error mean square that was half that of the other rates and therefore, more cultivars could be separated by using it. Additionally, all of the Group II cultivars did not have a constant rate of taproot elongation, as is implied by the data in Table 6. For example, some cultivars with relatively slow standard rates of taproot elongation had relatively fast rates during the first 7 days after planting and progressively slower rates thereafter. Thus, allowing elongation of at least some cultivars to 177 cm not only reduces the variability of the taproot elongation rate measurement, but allows the expression of cultivar differences in rate that might not be expressed during shorter periods of growth. Consequently, taproot elongation rates determined over shorter time intervals probably could be used for preliminary screening of cultivars, but a final screening should allow some cultivars to elongate at least 177 cm. Furthermore, investigations of taproot elongation at later stages of growth using even longer tubes might be useful in the final stages of selection.

Seed Weight Experiment

Burris et al. (1971) found that soybean seedling taproot length at 7 days after imbibition decreased with decreasing seed size. Similarly, seed weight in the present experiment also influenced taproot elongation, even though seed weight was not correlated with differences in taproot elongation rates among cultivars. Plants grown from seeds

Table 6. Correlation coefficients, based on cultivar means, between taproot elongation rates by the standard method and elongation rates during shorter time intervals, along with means and ranges of values (n = 105)

	Correlation coefficient with elongation rate	Mean	Range
		$cm \cdot day^{-1}$	$cm \cdot day^{-1}$
Standard elongation rate	--	4.13	3.00-5.29
Rate 0-14 days	.89**	3.68	1.89-5.12
Rate 0-21 days	.96**	3.81	2.22-5.02
Rate 0-28 days	.99**	3.98	2.61-5.24
Rate 0-7 days	.75**	3.69	1.89-4.93
Rate 7-14 days	.93**	3.77	1.59-5.79
Rate 14-21 days	.91**	4.09	2.61-5.59
Rate 21-28 days	.89**	4.48	2.96-6.04

**Significant at the .01 level.

that were heavier than the average seed weight had taproot elongation rates of 4.40 $cm \cdot day^{-1}$, compared with 4.22 $cm \cdot day^{-1}$ for plants from lighter than average seed (Table 7). Cultivar differences, however, were much greater than seed weight category differences. For example, Magna and Manchu had faster rates of taproot elongation than Vickery and Kanro, regardless of seed weight.

The effects of seed weight category, cultivar, and the cultivar by seed weight category interaction were all significant ($P < .01$). Vickery had a much greater reduction in the taproot elongation rate at the lighter seed weight than did Magna, which showed the least reduction. But, Kanro, which has a relatively heavy average seed weight, and Manchu Madison, which has a relatively light average seed weight, both had about the same reduction in rate between the heavy and light seed weight categories. Obviously, taproot elongation rates of 'average-seeded' cultivar types are not necessarily reduced to a greater extent than 'large-seeded' cultivar types by lighter than average seed weights, even though 'average-seeded' types presumably have less stored carbohydrates than 'large-seeded' types. Burris et al. (1971) found that percentage of cotyledonary dry weight loss was inversely proportional to seed weight, but there was no significant cultivar by seed size interactions. In fact, approximately the same amount of dry matter was lost from all seed size classes used in that study, indicating that the greater cotyledonary food reserves of heavy seeds were not completely responsible for the faster taproot elongation rates of those plants. Most likely, other substances exported by the

Table 7. Taproot elongation rates over 35 days for soybean seedlings grown from 'heavy' or 'light' seed of four cultivars (Error s^2 = 0.016; Error df = 49)

Cultivars	Selected Seed Weight Category ($g \cdot seed^{-1}$); (n = 8)		Cultivar means (n = 16)
	$cm.day^{-1}$		
Large-seeded types	.320g < Heavy < .340g	.220g < Light < .240g	
Magna	4.68	4.65	4.67
Kanro	4.18	3.99	4.08
Average-seeded types	.190g < Heavy < .210g	.090g < Light < .110g	
Manchu Madison	4.60	4.43	4.52
Vickery	4.15	3.80	3.97
Weight Range Means (n = 32)	4.40	4.22	

cotyledons can influence root growth (Evans, 1979) and are involved in these processes.

Plants grown from seed in the heavier categories had greater leaf areas and shoot dry weights than plants produced by the lighter seed. Plants with larger leaf areas may photosynthesize more than plants with smaller leaf areas, and therefore, have more carbohydrates available for root growth. The variations in plant size, however, can not completely explain the differences in the taproot elongation rate caused by seed weight. In fact, Burris et al. (1973) found that soybean seedlings grown from smaller seeds had smaller unifoliolate and cotyledonary surface areas than plants produced by larger seed, but had greater photosynthetic rates on an area basis and actually fixed more CO_2 than plants grown from larger seed at 7 days after imbibition. Thus, seed weight is an important factor when measuring taproot elongation rates, and the effect of seed weight can not be explained entirely in terms of increased carbohydrate supply. Even though effect of seed weight is small compared to cultivar differences, only seed of average size or weight should be used when evaluating and comparing cultivars for their taproot elongation rates.

Seed Source Experiment

Fehr and Probst (1971) found that seed source caused differences in yield, plant height, lodging, and date of maturity for ten soybean strains. Three sources of Wayne evaluated by Taylor et al. (1978), however, did not have significantly different rates of taproot

elongation. In the present experiment, taproot elongation rates of soybean plants from nine combinations of source, year of production, and cultural treatments of Wayne seed did differ significantly (Table 8). Furthermore, by using single degree of freedom comparisons, we determined which combinations of source, year, or cultural treatment caused a reduction in taproot elongation. For example, when the four 1979 seed lots from Castana, Iowa were compared, the taproot elongation rate of plants from seeds produced in 25 or 100 cm rows did not differ. But, elongation rates of seedlings from seed produced in irrigated and dryland plots averaged 4.18 and 4.37 $cm \cdot day^{-1}$, respectively, and were significantly different.

The four 1979 seed lots from Castana, Iowa were produced in an experiment described by Mason et al. (1980). They found that the irrigated plots produced smaller, poorly-filled seeds with imperfect seed coats, when compared to the dryland plots. Mason et al. (1980), speculated that, because the dryland plots matured earlier than the irrigated plots, seed fill and maturation of the dryland plots was less affected by the abnormally cool, wet weather that occurred in the late August and early September, 1979. Clearly, seed weight was not the cause of the elongation rate differences between plants from irrigated and dryland seed (Table 8), because only large seeds were used and seed weight did not differ. Furthermore, the leaf area and shoot dry weight of plants from irrigated or dryland 1979 seed did not differ either. Consequently, seedling taproot elongation may have somehow been influenced by the different environmental conditions the seed lots were

Table 8. Taproot elongation rates over 35 days for Wayne from nine combinations of source, year of production, and cultural treatment (Error s^2 = 0.034; Error df = 49)

Production Source	Year of production	Row width	Irrigation	Avg. seed weight	Taproot elongation rate
		cm		($mg \cdot seed^{-1}$)	($cm \cdot day^{-1}$)
Iowa Certified Seed	1976	--	--	174	4.23
Castana, IA.	1979	25	Yes	223	4.11
Castana, IA.	1979	25	No	215	4.34
Castana, IA.	1979	100	Yes	214	4.24
Castana, IA.	1979	100	No	219	4.39
Ames, IA.	1980	100	No	225	4.49
Castana, IA.	1980	100	No	217	4.28
Greenhouse	1980	pots	Yes	159	4.25
Puerto Rico	1980	100	No	206	4.49

exposed to during maturation. For example, Harris et al. (1965) reported that soybean seedling vigor was reduced in seed produced at locations with high mean temperatures during the last 45 days of maturation.

The single degree of freedom comparisons also revealed several other significant differences among the Wayne seed lots. Specifically, seed produced in Ames in 1980 had faster rates of taproot elongation than 1980 seed from Castana, and the average rate of all four 1980 seed lots was greater than that of 1976 seed. Furthermore, glasshouse grown seed had slower rates of elongation than field-produced seed from Ames or Puerto Rico. Obviously, even using these comparisons, it is impossible to determine whether source or location of production, age of the seed (Torrie, 1958), seed coat quality (Green et al., 1966), seed weight, or cultural or environmental factors during seed production are primarily responsible for the differences in taproot elongation among the nine Wayne seed lots. But, these seed lot differences, although small compared to cultivar differences, do emphasize the advantage of reducing the bias due to seed source by growing all test lines in one common environment immediately preceding evaluation, as suggested by Fehr and Probst (1971).

Depth of Planting Experiment

Depth of planting usually determines how much of the soybean stem will remain underground after emergence. Generally, the longer the portion of the stem below the soil or root medium surface, the greater

the number of secondary roots initiated from this region of the stem (unpublished observations). These secondary roots may compete with the taproot for carbohydrates and thus, may limit the rate of taproot growth. In fact, planting depth does cause a significant ($P < .01$) reduction in the rate of taproot elongation (Table 9). No attempt, however, was made to determine the number of secondary roots initiated on the underground portion of the stem. Consequently, a causative relationship between increased secondary root growth and decreased taproot elongation can not be established.

All plants emerged within a two day period, so rate of emergence was probably not a factor. Seed planted 3 cm deep, however, did produce plants with significantly greater leaf area and shoot dry weight than plants from seed planted at 6 and 9 cm. No conclusions, however, can be inferred from the relationship of taproot elongation rate and leaf area or shoot dry weight.

The four cultivars all responded to planting depth in the same way. Consequently, planting depth should not affect the evaluation of soybean lines, if all the lines have the same seed depth distribution. Only four cultivars were examined in this study, however, and a cultivar by planting depth interaction may exist for other cultivars. In the field, planting depth may be more important because of soil physical factors, such as soil crusting, which restrict emergence and may have a detrimental effect on taproot elongation.

Table 9. Taproot elongation rates over 34 days for four soybean cultivars planted at three depths (Error s^2 = 0.035; Error df = 169)

Cultivars	Planting depths ($n \geq 14$) 3 cm	6 cm	9 cm	Cultivar means ($n \geq 45$)
		($cm \cdot day^{-1}$)		
Magna	4.60	4.53	4.36	4.49
Kanro	3.77	3.69	3.63	3.70
Manchu Madison	4.45	4.34	4.18	4.32
Vickery	4.14	3.99	3.86	4.00
Planting Depth Means ($n \geq 63$)	4.24	4.14	3.99	

Seedling Damage Experiment

Soybean seedlings are often damaged in both the field and the glasshouse by insects or disease organisms. Furthermore, soil crusting, weather, or handling during measurements can also cause mechanical damage to the seedling either before or after emergence. Damage to soybean seedlings often results in the loss of one or more plant parts, which may hinder taproot elongation and plant growth, in general. To investigate the effect of seedling damage, various plant parts of four soybean cultivars were removed 8 days after planting and the taproot elongation rate was measured over a 40 day period (Table 10). Both cultivar and seedling damage effects were significant ($P < .01$). The treatment by cultivar interaction, however, was not significant indicating that the four cultivars generally responded to the damage treatments similarly. Magna and Manchu Madison had significantly faster taproot elongation rates than both Kanro and Amsoy 71, regardless of the treatment. Additionally, Kanro had a faster mean rate than Amsoy 71. All of the seedling damage treatments, except for removal of the shoot apex, significantly reduced the taproot elongation rate compared to the control. Removal of the shoot apex and both unifoliolates, however, resulted in a significantly slower taproot elongation rate than removing just the two unifoliolates.

Examination of the taproot elongation rate over 4 to 8 day intervals from planting to 40 days afterward (Table 11), revealed that removal of the shoot apex reduced taproot elongation rate between 22 and 36 days after planting. But, because the rate between 8 and 15 days

Table 10. Taproot elongation rate over 40 days for four soybean cultivars subjected to five seedling damage treatments (Error s^2 = 0.054; Error df = 124)

Cultivars	Seedling Damage Treatments - Parts Removed ($n \geq 6$)						Cultivar means ($n \geq 37$)
	Control	One unifoliolate	Two unifoliolates	Two cotyledons	Shoot apex	Shoot apex + two unifoliolates	
	$cm \cdot day^{-1}$						
Magna	3.99	3.66	3.39	3.57	3.86	3.11	3.57
Kanro	3.61	3.50	3.01	3.17	3.43	2.77	3.24
Manchu Madison	3.93	3.89	3.30	3.72	3.84	3.00	3.59
Amsoy 71	3.28	3.24	2.61	3.21	3.15	2.28	2.91
Treatment Means ($n \geq 23$)	3.72	3.56	3.06	3.41	3.61	2.79	

after planting, immediately after removal of the shoot apex, was faster than that of the control, the standard taproot elongation rate was not significantly different from that of the control. On the other hand, removal of two unifoliolates caused an immediate reduction in taproot elongation between 8 and 29 days after planting. When both the shoot apex and two unifoliolates were removed, rate of taproot elongation was significantly slower than that of the control throughout the 40 day measurement period.

One possible explanation for the changes in taproot elongation rate caused by removal of the shoot apex is that removal of the shoot apex altered the carbohydrate supply to the roots. Brouwer (1962) concluded that carbohydrate supply limits root growth more than shoot growth and that any treatment that increases the utilization or reduces the production of carbohydrates by the shoots will decrease root growth relatively more than shoot growth. At first, removal of the shoot apex would have decreased utilization of carbohydrate by the shoot. Later, after the two new shoots produced from buds in the axils of the unifoliolates began to grow, shoot demand for carbohydrates would have increased and the rate of root growth probably should have decreased. In fact, plants that had their shoot apex removed, generally had greater leaf areas and shoot dry weights than the control plants (control: 1601 cm and 6.6 g; shoot apex removed: 1706 cm and 7.1 g). Further studies are needed, however, to confirm this hypothesis.

Removal of both unifoliolates reduced the taproot elongation rate of all four cultivars evaluated. Removal of one unifoliolate, however,

Table 11. Taproot elongation rates for specified time periods as affected by seedling damage 8 days after planting

Seedling damage treatments - parts removed	Taproot Elongation Rate during specified periods (days after planting)						
	0-8	8-15	15-22	22-29	29-36	36-40	0-40
	cm•day^{-1}						
Control	3.34^{a†}	4.55^{b}	4.93^{a}	2.38^{a}	3.47^{a}	3.68^{ab}	3.72^{a}
One unifoliates	3.15^{ab}	4.29^{b}	4.83^{a}	2.33^{ab}	3.38^{a}	3.62^{ab}	3.56^{b}
Two unifoliates	3.38^{a}	2.32^{d}	3.83^{b}	2.16^{c}	3.47^{a}	3.80^{a}	3.06^{d}
Two cotyledons	3.31^{a}	3.62^{c}	4.61^{a}	2.28^{abc}	3.36^{a}	3.57^{ab}	3.41^{c}
Shoot apex	3.26^{ab}	4.94^{a}	4.85^{a}	2.15^{c}	3.09^{b}	3.51^{ab}	3.61^{ab}
Shoot apex + two unifoliates	2.88^{b}	2.47^{d}	2.99^{c}	2.19^{bc}	3.10^{b}	3.47^{b}	2.79^{e}

†Values within columns followed by the same letter are not significantly different at P = 0.05 by the DNMR test.

had a significant effect only on Magna. Partial defoliation can cause decreases in root growth relative to shoot growth until the equilibrium between root and shoot dry weight is re-established (Brouwer, 1962). Furthermore, removal of either one or both unifoliolates, before the first trifoliate has unrolled (VC) is a drastic reduction in leaf area and, probably, reduced the production of carbohydrates by the shoot. There is no obvious reason why removal of one unifoliolate affected Magna and not the other cultivars.

Finally, removal of both cotyledons significantly reduced the taproot elongation rates of Magna and Kanro. Weber and Caldwell (1966) reported that removal of the cotyledons at emergence reduced soybean yield by 8.5%, but removal of the cotyledons after the unifoliolates were fully expanded had no effect. In the present experiment the cotyledons were removed before full expansion of the unifoliolates, but only two of the four cultivars were affected. Apparently, the cotyledons of Magna and Kanro represented a more indispensable source of stored carbohydrate and (or) photosynthetic surface area than those of Amsoy 71 and Manchu Madison did. Magna and Kanro did have much greater seed weights than either Amsoy 71 or Manchu Madison. The cotyledons may also supply other factors important to taproot growth that were presnt in only the cotyledons of Magna and Kanro. In summary, the seedling damage experiment indicates that shoot damage does adversely affect taproot elongation. Furthermore, additional studies of this kind may improve the understanding of relationships between shoot and root growth.

CONCLUSIONS

Shoot growth characteristics and seed weight can not be used as preliminary selection criteria to find soybean cultivars with rapidly elongating taproots. The time required for evaluating soybean taproot elongation rates, however, can be reduced to 14 or 21 days, at least for initial screenings.

Taproot elongation rates are influenced by seed weight, seed source, depth of planting, and mechanical damage to seedlings. When selecting soybean cultivars or lines on the basis of their taproot elongation rates, the seed used should have been produced in a common environment, and should be of good quality and average weight. Care should be taken to insure that all lines evaluated have the same planting depth distribution and that all damaged seedlings are removed. Obviously, further study of the physiological processes controlling taproot elongation is needed, but with these precautions the method of Kaspar et al. (1982) can be used to screen soybean cultivars for rate of taproot elongation.

GENERAL SUMMARY AND CONCLUSIONS

Taylor et al. (1978) developed a glasshouse procedure for evaluating taproot elongation rates of soybean cultivars. One objective of the present study was to standardize the procedure of Taylor et al. (1978), so that other scientists using this procedure would obtain comparable results. To accomplish this, medium-grade horticultural vermiculite and daily watering with a double strength modified Hoagland's solution were substituted for the soil used by Taylor et al. (1978). A 15.5 h photoperiod was maintained and supplemental lighting was provided to reduce variability due to seasonal changes in daylength. Additionally, some taproots were allowed to elongate 177 cm to permit full expression of cultivar differences.

Using the modified technique, taproot elongation rates of 105 soybean cultivars from three maturity groups were evaluated. Large differences in the rate of taproot elongation were found among cultivars within a maturity group. Small variations in the relative response of some cultivars were found, but these variations do not present a major problem for use of this method in a screening program. Much of the variation was thought to be associated with differences in seed quality.

The second major objective of this study was to determine whether soybean cultivars with widely differing taproot elongation rates in the glasshouse have different patterns of root growth and water extraction in the field. Eight soybean cultivars, four with relatively fast rates of taproot elongation and four with slow rates, were planted in the field. Using the core-break technique, cultivars with fast taproot

elongation rates were found to have slightly deeper maximum rooting depths than those with slower elongation rates. Furthermore, the cultivars with faster elongation rates tended to have a greater root length density deeper in the soil profile than the slow elongating cultivars. The differences in maximum rooting depth and relative root length density with depth, however, were not always statistically significant.

More conclusive evidence of the deeper root system of cultivars with fast taproot elongation rates was provided by water use data. In general, cultivars with fast taproot elongation rates obtained a significantly greater percentage of their water from deeper in the soil profile than did cultivars with slow taproot elongation rates. Total water use for all cultivars, however, was nearly the same, probably because rains in late August and early September rewetted the upper 30 cm of the profile.

Another objective of this study was to determine whether the time required to evaluate taproot elongation rate of cultivars could be shortened. Taproot elongation rates over short time intervals correlated well with rates determined over longer intervals. Allowing some cultivars to elongate 177 cm, however, permitted more cultivars to be separated on the basis of their taproot elongation rates. Furthermore, taproots of some cultivars do not elongate at a steady rate throughout their vegetative growth. Thus, short time intervals could be used for preliminary screenings of cultivars, but a final screening should allow some cultivars to elongate 177 cm or more.

The number of cultivars or lines that can be screened could be increased if an easily measured characteristic that is closely correlated with taproot elongation were used as a preliminary screening criterion. Correlation coefficients, based on cultivar means, between elongation rate and plant height, shoot dry weight, leaf area, and seed weight were determined, but only plant height was significantly correlated with taproot elongation rate. The relationship, however, was not strong enough to permit use of height as a preliminary screening criterion for taproot elongation rate.

Lastly, the effects of planting depth, seed weight, seed source, and seedling damage on taproot elongation were studied. All of these factors were found to influence taproot elongation rate. Therefore, attempts should be made to minimize their effects, to reduce experimental error. Cultivars to be evaluated should be grown in a common environment in the generation immediately preceding evaluation, and only seed of average weight and of good quality should be used. All cultivars also should have the same planting depth.

Collectively, the research presented in this dissertation shows that it is possible to select plants with rapidly elongating taproots, and thereby perhaps, improve drought avoidance of soybeans.

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